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BOTANY

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J. REYNOLDS GREEN
Sc. D., F.R.S.

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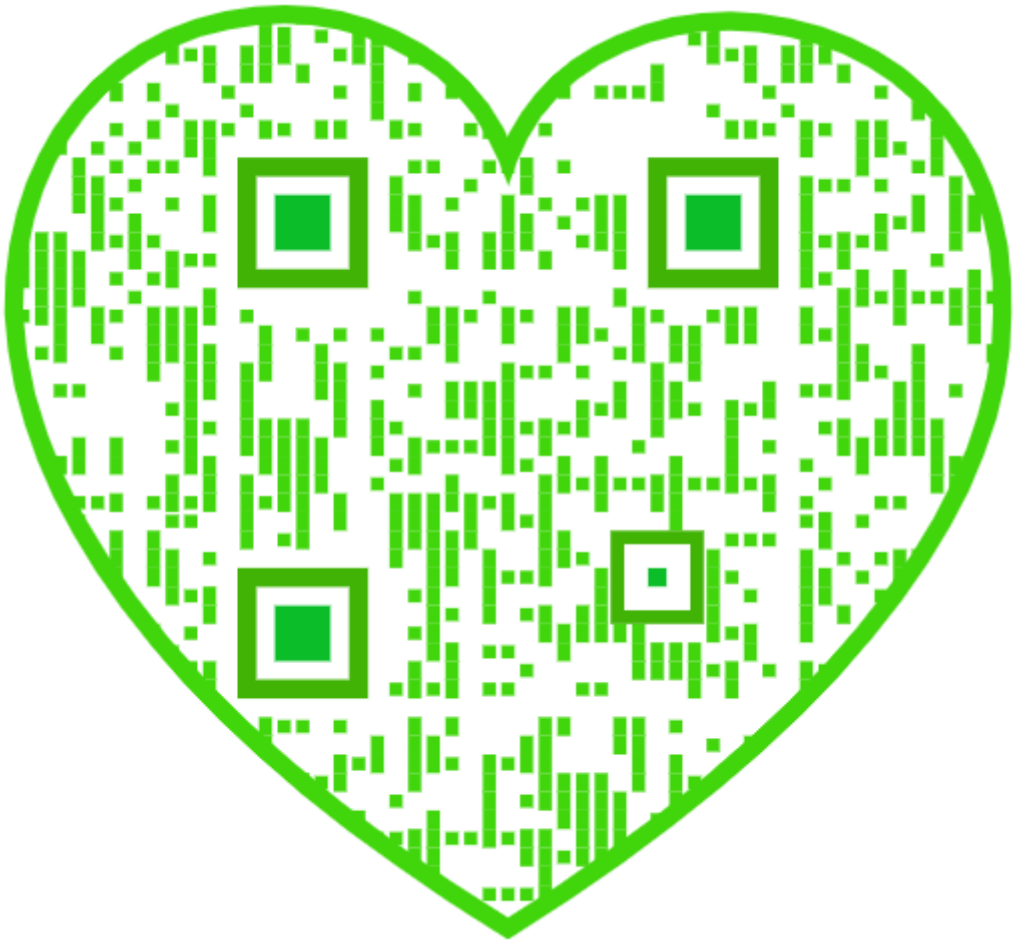
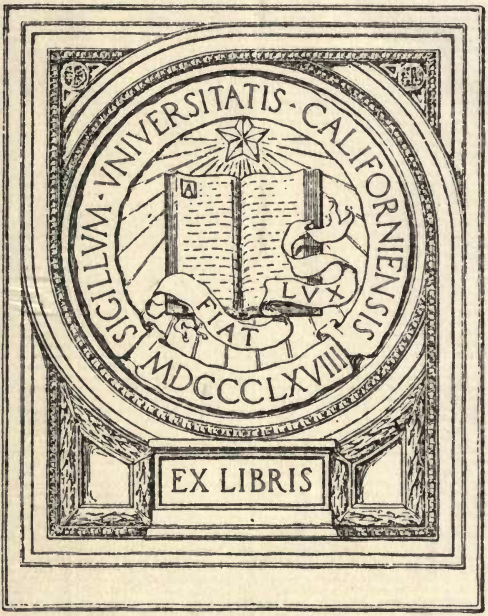


IN MEMORIAM
Richard M. Holman



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BOTANY

Appleton's Scientific Primers

Edited by J. Reynolds Green, Sc.D., F.R.S.

BOTANY

BY

J. REYNOLDS GREEN, Sc.D., F.R.S.

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IN MEMORIAM
Richard M. Holman

PREFACE

In writing this little introduction to the study of a plant I have endeavoured especially to present it to the reader as a living organism. Botany is now regarded as a branch of biology, and is not satisfactorily studied by gathering plants and, after ascertaining their names and the natural orders to which they belong, drying them and putting them away in a cabinet. I have tried to present them as they are engaged in the struggle for existence, and to call my readers' attention not only to their form and structure but especially to what they do in life, and *why* and *how* they do it.

I hope that those who study them by the assistance of this little primer will try to have the living plant under observation while they read it. I have not written any detailed scheme of laboratory work, but I hope my readers will be able to construct such a scheme for themselves as they follow the directions for study given in the text.

I should like to suggest that students should read the Chemistry primer first, to gain some acquaintance with the phenomena underlying the processes of construction and decomposition going on in the plant. It would be well to read the Biology primer also before beginning Botany.

J. REYNOLDS GREEN.

Cambridge, 1909.

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BOTANY

CHAPTER I

INTRODUCTORY

Of all the things we see about us as soon as we escape from the life and surroundings of the town, none is more familiar to us than the common green plant. We tread upon grass and other plants which clothe the earth's surface, we walk under trees, around bushes, and by the sides of hedges, or we wander through more cultivated scenes, enjoying the beauty and fragrance of the well-cared-for garden. In all this wealth of vegetation perhaps, however, one fact sometimes escapes our notice. These plants, trees, shrubs, weeds, or what not are *alive*. We do not deny this when we hear it said, but the idea is hardly a prominent one in the view we take of things in general. It is based probably on the fact that we do not see the plants move, except as their slender twigs and branches or their numerous leaves are swayed to and fro by the wind, for to our own somewhat narrow experience life is so closely connected with restless change of position or locomotion. Yet if we wish to study plants to learn something more about them than a casual glance can tell us, we must bear in mind these two facts on which their whole story turns: first, they are living creatures; second, they spend their lives in the same place in which they commenced them. This is true of the greater number of plants we see around us, though there are some exceptions, chiefly

plants which, living in water, are passively moved about by the currents of the stream.

The fact that a plant is alive and conducts itself as a living organism implies certain things. It must receive suitable and sufficient nourishment; it must possess a certain power of adjusting itself to its surroundings, defending itself against possible dangers and overcoming definite difficulties which these surroundings occasion, and taking advantage of such benefits as are met with in them. It must possess, to at any rate a limited extent, a power of appreciating its relations to such surroundings, of realising variations in certain of them, such as light, moisture, and temperature, that it may adapt itself accordingly.

The second fact, that it cannot alter its position by moving freely about, makes those requirements more essential. It also demands that it shall be possessed of such a safe attachment to its situation as shall secure it an appropriate position and shall enable it to enjoy undisturbed such advantages as the surroundings offer. Further, it calls for a certain power of adjustment of its various parts to the air above it and the earth in which it is fastened, as changes in both of them are frequent and sometimes violent. As the only sources of nourishment possible to it are the air and the soil, together with the water which both contain in constantly varying amount, its construction must be such that the same parts which secure anchorage or support shall be capable of securing supplies of the various materials which ultimately become the medium of nourishment.

A further requirement of every living organism is the need of possessing the means of bearing offspring which shall succeed it in the great scene of nature. To a stationary organism this introduces difficulties from which the readily moving animal is free, but these difficulties have been overcome by adaptations to the habit

of life which are among the most complicated and the most perfect that nature shows us.

So the life of a plant shows us conflict and struggle waged against disadvantages of a very formidable nature; a power of appreciating difficulties and of struggling against them; further, it exhibits a capacity of seizing upon such advantages as present themselves, not only in the air and in the soil, but in relative association and competition with each other.

We are familiar with the fact that part of an ordinary green plant is embedded in the soil. Such a part is commonly known to us as its *root*, and we distinguish it in several ways from the part which rises into the air (Fig. 1). In the case of plants which live in water we find much the same division of the plant body. There is in their case also a root part, which is not green and which is buried in the soil or mud at the bottom of the water; there is a part which stretches up into the water, in some cases extending into the air above the surface. We often express this fact by saying that the plant is differentiated into a root and a shoot. This differentiation is a fundamental one, for the two parts behave very differently. They always grow in opposite directions, and as these directions are generally upwards and downwards they are spoken of as the *ascending* and the *descending* axes of the plant.

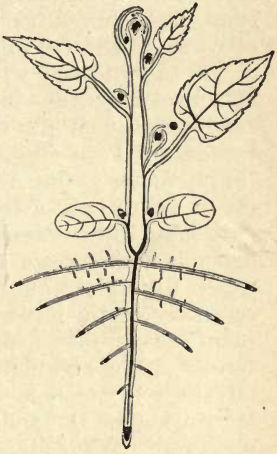

FIG. 1. Diagram showing the general structure of a dicotyledonous plant.

We need not at present consider very fully the case of the water-plant, and will therefore examine the relations between the root and shoot in general and the surroundings in which each finds itself.

The anchorage of the plant is secured by the penetration of the soil by the roots. The advantage thus secured is not obtained without difficulty and even danger. To become fixed in the soil the plant must penetrate it, a process which it can only carry out by its gradual growth. The composition of the soil offers certain difficulties to this penetration: it may be too dense or too powdery, too dry or too wet; it may be slimy like clay, or very hard and strong. The amount of water in the soil and the degree in which it contains air are also factors which must be taken into account in considering this growth. After a plant has once established itself and secured firm anchorage, it still has to deal with varying conditions of a similar nature, for the character of the soil is very liable to changes, depending on conditions of temperature, weather, and so on.

Besides the advantage of a firm anchorage, the root depends upon the soil for the supply of certain materials which ultimately aid in some way in its nutritive processes. Certain minerals are necessary to every green plant, many others are advantageous, some are deleterious. We are here face to face with dangers and advantages which need adjustment to the plant as it is growing in the soil. Such a struggle can be easily observed. While all plants need compounds of nitrogen, some will only flourish on soil which contains as well a certain, often a large, proportion of chalk, others fail entirely if the chalk is plentiful. It is much the same with other constituents of the soil.

If a plant is growing in uncongenial surroundings it has but little power of adjustment to them. It consequently dies out more or less rapidly. If on the other

hand its environment suits its constitution, it has to adapt its structure to the duty of absorbing from the soil what the latter will afford. So the two duties of anchorage and absorption exist together, and the differentiated root system necessarily discharges both.

If we turn to inquire what dangers beset the part of the plant we have called the shoot, which grows up into the air and forms a head that is frequently of large size, we find them taking shape in the various atmospheric changes incident to every climate. First of these we may place wind or tempest. As the shoot body grows it must offer more and more resistance to air currents, a resistance which may easily culminate in a violent uprooting of the plant. This involves such a subdivision of the plant body as will allow the wind to penetrate through it without serious disturbance. Here we see one meaning of the tapering boughs and twigs, which become more and more flexible as they become increasingly slender. In the central part of the shoot system they are rigid and can resist the storm; where by their dimensions resistance becomes impracticable we find flexibility, enabling them to bow to the wind often so completely as to place their long axes parallel to the direction in which it is blowing.

Yet another reason for this continued subdivision of the plant body is found in its relation to the absorption from the soil which we have found associated with the root. The latter is continually absorbing the water of the soil; after separating from such water the mineral constituents it contains, a very large part indeed of the water is evaporated, and so passes away to the exterior again. To favour such evaporation it is advantageous that the ratio between surface and bulk shall be a large one, and so the great subdivision of the subaerial part of the plant is concerned in solving the problem of its nourishment.

Indirectly the composition of the above-ground part of the plant has a direct application to a danger to which the underground region is exposed. The pressure of the wind upon an unyielding surface in the air would be attended by great danger to the anchoring root, which might be violently pulled from the ground by the leverage exerted by such pressure. The great subdivision of the shoot system and the flexibility of its ultimate twigs minimises this danger, but even as it is, it is not unusual after a tempest to find even sturdy trees uprooted and thrown down.

The distribution of the water of rain-storms presents another problem which must be solved by the shoot system. The water can be led either towards or away from the centre of the plant. Should the root system be one which spreads considerably and extends to long distances below the surface of the soil, it is of great importance that the rainfall collected on the central mass of shoots shall be distributed widely so as to reach as far as the extremities of the roots, watering in this way a large area of ground. If the root system consists of a strong main root with comparatively few branches, this arrangement would largely deprive it of water. Hence in plants with roots distributed in this way we find arrangements to conduct the water into the centre of the mass of shoots.

In some rare cases the duty generally discharged by the root as an anchoring organ falls upon the shoot, which then is partly developed underground. Such a stem bearing in its turn appendages has a special name —it is called a rhizome.

If we pass to a closer study of the much divided or branched shoot we find almost invariably that its ultimate twigs put forth certain regularly arranged flattened expansions. In cases where there is much exposure to currents of air, these flattened portions are furnished

with stalks of variable length which are extremely flexible and allow the flattened organs to sway freely backwards and forwards as the wind blows upon them. These flattened portions, further, are usually of a vivid green colour; they are then known as *leaves*, or, preferably, *foliage leaves*.

As almost all plants possess leaves we may inquire why these organs should so uniformly be thin and flat.

There are several reasons of almost equal importance. The leaf or other winged part of the shoot portion is in contact or relation with the air only. Interchanges of gases between the air and the leaf are continually going on, and these interchanges are effected most easily and fully with a large extent of surface. No form gives so much surface in proportion to its bulk as a thin flat plate, just such a form indeed as the flattened portion or *blade* of the leaf. The interchanges include the absorption of particular gases from the air, and the giving out of gases and water vapour. As we shall see later, the internal structure of the leaf-blade is arranged largely with a view to the carrying out of these exchanges.

A second reason for the flattening of the leaf is concerned with the manufacture of the plant's food. A particular gas known as *carbon dioxide*, which is taken in from the air, is ultimately built up into a true food material, a kind of sugar. Though the formation of sugar in the plant is not fully understood, it is known to depend upon the presence of the green colouring matter and its being properly illuminated. The flattened form helps to secure the arrangement of the green colouring matter in such a way that the light, either of direct sunshine or of the less bright diffused daylight, may reach it with the least obstruction.

Yet a third reason may be given. The leaves are very frequently so placed that they extend outwards from the plant and lie nearly parallel to the surface of

the ground. In this way they present their edges to the wind, and offer as little obstacle as possible to its passage through the tree, so making as small as possible the risk of being torn off when the force of the wind is strong. As the wind passes between them they are made to rise and fall, but they offer much less resistance to its force than they would if they were not flattened.

The arrangements of the plant and its parts so far as we have studied them are such as to secure its firm attachment to the soil, its stability in storms, with relation both to wind and rain. They also make possible the absorption of liquid, containing mineral matters, from the soil; the evaporation of the excess of water so absorbed; the free interchange of gases between it and the air; the needed facilities for the manufacture of sugar from the gases absorbed from the air and the water from the soil. They are, in fact, suitable to support and nourish a stationary living organism and to furnish defences against the most evident dangers to which it is exposed.

The establishment of such a position by the plant is carried out by means of growth alone. It is a gradual process, therefore, and must be accompanied by the nutritive processes which enable growth to take place First among these comes the supply of the material for the increase of size which we associate with growth. We have seen that the plant absorbs from the soil certain mineral compounds dissolved in water, and from the air certain of its constituent gases. The most important of the materials which the earth yields are nitrates of potassium, calcium, and other metals, phosphates of the same, traces of compounds of iron, a little silica in some combination, together with the water in which they are dissolved; carbon dioxide is supplied by the air. When the absorption of these substances is possible, and when light is sufficient and temperature

moderate, the healthy plant is found to increase in size, and gradually to show all the phenomena of growth. Hence these various compounds have been regarded as its food. This is not, however, a correct view, for they should be considered only as raw materials from which the green plant can make the food it needs. This is effected by the agency of the green colouring matter, the so-called *chlorophyll*, but only when it receives an appropriate amount of light. In the absence of chlorophyll or in insufficient light the supply of all these various compounds does not afford any nourishment to the plant. Plants without chlorophyll are not far to seek; we find them in the mushrooms, in the moulds that grow so readily on decaying matter, the mildews of corn and other crops, and so on. These cannot develop at all when supplied only with the inorganic compounds mentioned.

The plant then in order to grow and to establish itself has to be provided with suitable food. If it has chlorophyll and is properly illuminated it makes this food for itself from the inorganic materials the soil and air provide. Plants which cannot make their food have to obtain it from living or dead organic matter. Though this is difficult it is not impossible, for such matter abounds almost everywhere—not only in the soil but in the numerous manufactured products which we meet with all around us. Living organisms also are often made to yield food to these non-green plants. The chlorophyll-containing plants are continuously making the organic substance which constitutes their food as long as light shines upon them. We find them growing at its expense and accumulating large quantities of such substances as sugar, starch, proteins, and fats in their own bodies. As they in their turn, or many of them, ultimately become the food of animals, we may see their importance in the *rôle* of nature. The fact is that

the green plant is the only organism which has the power of forming organic substance from the inorganic material of the earth and air. As all living beings are dependent on this organic substance for the maintenance of life, we see how the continuation of life itself upon the earth depends on the activity of the green plant.

The establishment of the position of the plant and its defence when so established may be seen, therefore, to be subordinate to the manufacture of organic food.

The food so made is complex in character and will be dealt with in greater detail in a subsequent chapter. It comprises chiefly three classes of substance: *carbohydrates*, of which sugar and starch are representatives, *fats*, and *proteins*, which are much more complex in composition, and are represented by the white of egg and by the chief constituent of meat and fish. The proteins are held to be the organic material which most resembles the living substance itself.

As it is the process of growth at the expense of this newly constructed food, or of a small supply derived directly from its parent, by which the young plant makes its way into its appropriate position, it is clear that this is the action of a living organism and becomes probable that the surroundings of the plant affect it in other ways than by affording it the material from which to make its food. Careful observation shows that this is the case. The root of the plant at even its first appearance grows downwards in the direction of the soil. If it be made to point in another direction, its plan of growth slowly changes and it gradually curves till its tip is pointing downwards again (Fig. 2). If

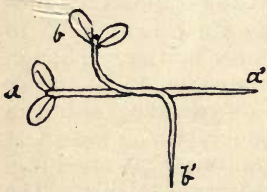

FIG. 2. Geotropic curvature in root and shoot of mustard. (Natural size.) (After Gibson.)

light reaches it, it bends slowly away from the illuminating ray; if anything comes into contact with its tip, growth causes it to curve so as to leave the obstacle on one side. The young root shows in these ways certain sensitivities, reacting to the incidents of its environment, and behaving as if it were possessed of rudimentary perceptions of direction, illumination, and contact. Other features of the environment also affect it, particularly moisture. The shoot in its behaviour shows similar phenomena, but its conduct when influenced, or, as it is generally called, *stimulated*, by gravity, light, or other disturbing causes, is as a rule the opposite of that of the root. It grows upwards against gravity; it curves towards and not away from light; its behaviour with regard to contact is not always uniform. Both parts, however, show what we claimed at the outset as one of its primal necessities, the power of adjusting itself to changes in its surroundings.

Consideration of the fourth requirement, the power to reproduce itself, must be deferred for the present.

We may now with advantage turn to the composition of the plant and ask what is the distribution in it of the living matter to which this behaviour is to be attributed.

It is best to begin the study of this point by examining quite a young plant, or preferably the seed of a plant, as the structure is then simple, while it becomes very complex as the plant grows. If we take a seed (Fig. 3) we find it contains a young plant or embryo, in which by careful dissection we can make out a young root and a young shoot. The shoot consists of a short axis, to which are attached either one or two leaves known as cotyledons, with perhaps traces of more leaves above them (Fig. 4). When we cut such a young root or young shoot, we find that it is made up of

FIG. 3. Section of a seed. *a*, embryo.

a large number of very small pieces of living substance, or *protoplasm*, each separated from its neighbours by a thin membrane or *cell wall* which surrounds it (Fig. 5). Very fine connecting threads of protoplasm extend through the cell walls and so join the little pieces of protoplasm together, but these are so delicate that it is not possible to see them without very skilful preparation.

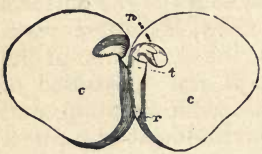

FIG. 4. Embryo of pea magnified. *r*, radicle; *n*, plumule; *c*, cotyledons.

The living substance thus extends throughout the plant in complete continuity, though it is apparently divided into a number of separate pieces by cell walls or membranes. These serve at the outset only for purposes of support, and form a kind of skeleton. Each little piece of protoplasm contains a small highly organised portion called its nucleus; the whole piece is called a protoplast; it is approximately cubical in shape and has a diameter of about 1-3000th of an inch.

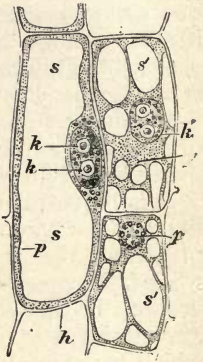

FIG. 5. Vegetable cells. *h*, cell wall; *p*, protoplasm; *k*, *k*, nucleus; *s*, vacuole. ×700. (After Sachs.)

As the little protoplast absorbs water and gets larger, entering into active life, it finds itself in need of constantly renewed supplies of water. Here is its first individual difficulty, for it is only the external cells which can come into contact with the water outside the plant. To overcome this difficulty the protoplast gradually forms a central cavity in its own substance, in which it holds a store of water. This cavity is known as a *vacuole*; it is of the greatest importance in the

maintenance of the life and the nutrition of the protoplast.

As the plant gets older and larger a considerable amount of differentiation of its internal substance becomes necessary. This we shall study later. Meantime we may say that these changes are accompanied by the death of some of the protoplasts. The membranes or skeleton of these protoplasts are left in the interior and subserve certain important purposes; but the protoplasts remain in full vigour towards the exterior and particularly towards the extremities of both shoots and roots, where new formation of them is continually taking place.

The living substance is thus situated in greatest amount towards the outside of the plant and at its extremities, where its contact with the environment can be most easily maintained. The subordinate mechanisms of its life, which are concerned with its mechanical support and with the efficient working of its body and the co-ordination of its various forces, are hidden away more deeply in its interior.

CHAPTER II

THE EARLY DEVELOPMENT OF A PLANT—THE GERMINATION OF A DICOTYLEDONOUS SEED

THERE is a great variety in degree of development among the plants which exist upon the earth. The most highly organised of these are the so-called flowering plants, to which most of the terrestrial forms belong.

These plants have a certain feature in common which distinguishes them from all others. They form *seeds*, which become separated from the parent and after a period of rest develop into new plants. A seed is essentially a very young plant in a dormant or resting

condition, clothed with a separable protective coat, and supplied with a certain quantity of food stored in it or around it by the parent from which it came. In its quiescent condition this young plant is called an *embryo*. It consists of a young root and a young shoot, the latter being composed of a stem on which are borne a certain number of leaves. These parts are known as the *radicle* and *plumule* respectively, the first-formed leaves being called *cotyledons*. The number of cotyledons varies; in most cases there are two, in others one, while in others again there may be several. The number of cotyledons is constant throughout large groups of plants and is associated with differences of structure of the other parts of the plant. The first two groups referred to are called Dicotyledons and Monocotyledons. In another group called the Gymnosperms we find a variable number, sometimes as many as fifteen.

The young embryo is fitted to bear separation from the parent and transport to different situations by the fact that its life is in a dormant state and that it is protected by the skin or testa of the seed. Under appropriate conditions it can resume active life and grow into an adult plant, provision having been made for its nutrition during the early stages of its development and until it acquires the power of making its own food. This necessary food is prepared by the parent plant and is originally deposited as a relatively bulky mass around the embryo in its early development in a particular cell known as the *embryo sac*. This food constitutes what is known as the *endosperm*, a collection of cells which fill up all the space in the embryo sac which is not occupied by the embryo.

The cells of the endosperm with their contents are all provided for the nourishment of the embryo. In some cases the embryo feeds upon this store while very immature and before it assumes its quiescent state. In

others its quiescence takes place very early, so that the endosperm remains unabsorbed around it and is not used till the resumption of active life and growth takes place. The difference in the time of this absorption influences the size of the embryo, which is naturally much larger when it has absorbed the endosperm. The food so absorbed is always deposited again in some part of the young embryo, very frequently in the cotyledons which become large and fleshy. Occasionally, as in the Brazil nut, it is stored in the axis of the embryo.

When the endosperm persists till the resumption of life by the embryo—the process known as the germination of the seed—the latter is said to be an *albuminous* seed (Fig. 6). If the embryo alone is present inside the skin (Fig. 7) it is called *exalbuminous*.

FIG. 6. Section of a seed. *a*, embryo.

It is best to begin the study of these seedbearing plants with the largest group, the Dicotyledons.

They furnish us with examples of both classes of seeds which are easily accessible and which germinate readily. We may take first the common bean. To examine the seed it is well to soak it for several hours in water, which is absorbed by the skin, so that the whole seed swells and its parts can be easily separated from one another. The seed is somewhat kidney-shaped, and bears on the concave part a scar at the point at which it was attached to the fruit from which it came. A little way from one end of this scar is found an aperture through the skin, known as the *micropyle*, through which the radicle emerges on germination. It can be localised by gently squeezing the soaked seed,

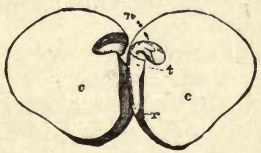

FIG. 7. Embryo of pea magnified. *r*, radicle; *n t*, plumule; *c*, cotyledons.

when a drop of water will ooze out of it. On removing the testa the body of the seed is found to consist of a very bulky embryo. The two cotyledons are large masses placed face to face and easily separated from each other. On gently moving them apart each is found to be attached to a very short axis which lies between them and is almost hidden when their faces are in contact. The lower end of the axis is the radicle and is bluntly pointed; the upper end, the plumule, which curls inwards between the cotyledons, bears two minute leaves.

We may compare with the bean a seed of about the same size, that of the castor oil plant. It must be soaked until it swells, when the hard coat it possesses will crack. On removing the latter a fleshy mass will be seen which cannot be separated into two portions without splitting it. If it is divided into two it will be found that the embryo plant consists of two very thin flat cotyledons lying in the centre face to face, with the very short axis (plumule and radicle) between them. The fleshy part of the seed surrounds the whole and adheres firmly to the backs of the delicate cotyledons. This mass is the endosperm, which has not been absorbed by the embryo during its early growth.

If the seed is soaked in alcohol this dissection is easier, as the parts do not then adhere so closely together.

After a period of variable length the embryo awakes from its quiescent or resting state and develops into a seedling, which goes on to become an adult plant. The quickening into this renewed activity, which is technically called its *germination*, is only possible when the external conditions become favourable. The process demands moisture, a moderate degree of warmth, and the presence of oxygen. It may be studied easily with a little care, as it can take place in an ordinary room. The absence of light is not essential, although seeds are usually buried in the soil before they germinate.

Having soaked a bean for several hours till it has become swollen, remove it from the water and keep it on damp boiled sawdust or in some moist situation in an ordinary room for some days. After a short time the young radicle will be found to protrude from the micropyle and to grow downwards. The cotyledons swell and the testa cracks and begins to slip off. The plumule, which was seen to be curved inwards, elongates; the curvature becomes more marked and forms a loop which emerges from between the cotyledons; it finally straightens itself and thenceforward grows vertically upwards. This loop is formed from the part just above the cotyledons which is known as the *epicotyl.* The cotyledons remain much as they were, but as the seedling grows their contents are gradually absorbed by the axis and they shrivel away. In their normal development when the seed is below the surface of the earth the cotyledons remain buried. The advantage of the looped epicotyl is seen as it presses upward through the layer of soil above the seed, for the delicate leaves of the plumule are saved from the injury which they would suffer if they had to force their way through the earth. The epicotyl in fact opens a passage for them.

Some seeds whose structure is almost identical with that of the bean behave a little differently in germination. The part of the axis which elongates and brings the plumule through the soil is a region a little *below* the cotyledons, and it is consequently called the *hypocotyl.* The lengthening of this part causes the cotyledons also to be carried up into the air, and after a short time they turn green, and take on the work of the foliage leaves which are developed as the plumule grows.

When the castor oil seed germinates the early stages are much the same as in those of the bean. The seed swells and the radicle grows through the micropyle, and very soon the young root branches freely. The endo-

sperm swells and the flat cotyledons which remain in contact with it begin to absorb the contents of its cells. The face of the endosperm becomes very slimy or mucilaginous and it continues to swell for some days, ultimately cracking and being loosely attached to the absorbing cotyledons. The hypocotyl grows up in the form of a loop and drags the cotyledons out of the soil with the endosperm clinging to them. They very quickly change colour, becoming yellow and ultimately green, and as the last traces of the endosperm are used up they grow out laterally and take on the appearance and the function of foliage leaves.

CHAPTER III

THE FORMATION OF THE ROOT SYSTEM

THE seeds just described are very useful for observing also the growth and development of the seedling. Even better material for this purpose is supplied by the seeds of the common cress. If several of these seeds are soaked in water and then scattered over the inside of a damp flower pot they will germinate very freely if the pot is kept moist and moderately warm, putting out their roots in a few hours. As they will have been sown quite indiscriminately, their positions will be irregular and the young rootlets will emerge at first in very different directions. If they are allowed to remain undisturbed as they elongate they invariably manage to direct their apices downwards, effecting sometimes curious curvatures to do so. This strange uniformity of behaviour suggests that the young seedling has a kind of appreciation of its position or the direction of its growth. We can test this suggestion by taking several of them from the positions they have assumed and placing them so that their roots are at different angles

with the vertical. So long as they are intact, they gradually modify their growth so as to make their apices again point vertically downwards (Fig. 8).

If we study the behaviour of the roots under various conditions we soon find that they manifest other forms of sensitiveness, all of which are brought to bear upon the problem of establishing themselves in the soil. When a root enters the latter and passes between the particles which compose it, it must sooner or later come into contact with some of them, and not improbably such contact will hinder the advance of the root in a straight or nearly straight line. The growth of the root is achieved by its advancing in a kind of corkscrew fashion, the tip describing a spiral rather than a straight line. This no doubt tends to push aside slight obstacles which may meet the advancing tip. If we experiment upon a seedling bean, which we have seen can be cultivated in moist air, we can imitate the conditions met with in the soil by attaching some small piece of a hard substance to one side of the root tip, using a little gum as the attaching medium. By this treatment we can ensure that the contact shall be prolonged, and hence the struggle between the root and the obstacle will be carried to such a point as to exhibit very striking effects. After a short time the growing region of the root, which is some little distance behind the apex, will be observed to curve in such a way as to turn the tip from the object touching it. As the pressure is not removed under the conditions of the experiment, this curvature will become very pronounced and after a day or two the root will be curled into a loop. In the soil so pronounced a curva-

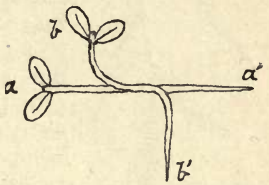

FIG. 8. Geotropic curvature in root and shoot of mustard. (Natural size.) (After Gibson.)

ture is not met with, as a slight change in the direction of growth causes the root to grow past the obstructing body, and then the downward direction is resumed.

We can thus show that the young root has not only an appreciation of direction, but it can in some way recognise when it is in contact with some solid obstacle and that it can modify its growth with a view to getting past such a body and penetrating further into the soil.

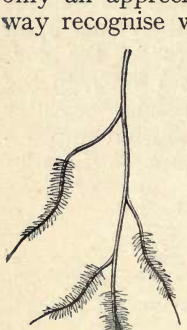

FIG. 9. Young roots showing root hairs.

The root further appreciates the incidence of a lateral light. If the seedling is cultivated in a glass vessel and so placed that light reaches it only on one side it very quickly modifies its growth so that the apex becomes turned away from the light. In the soil this behaviour brings it closer to the particles of the soil, especially a little way behind the tip. These three rudimentary senses or sensitivities are supplemented by a fourth. It shows an evident appreciation of the presence of moisture, and grows towards the dampest parts of the medium in which it is placed.

If we revert for a moment to the young cress seedling we find that when it has attained the length of about half an inch a number of long delicate outgrowths of its surface may be seen arranged in a broad band all round the root at a little distance behind the apex (Fig. 9). So long as the root grows this band of outgrowths, which are known as *root hairs*, is maintained. New ones are formed on the side of the apex while the older ones die and disappear on the hinder margin of the band. As the root advances in the soil these hairs become so closely attached to its particles that they cannot be

separated mechanically. While they thus aid materially in attaching the root to the soil, they carry on the absorption of the water of the soil with the mineral compounds dissolved therein.

It is customary to consider the influences we have spoken of, gravitation, contact, light, and moisture, as *stimuli*, and to speak of the behaviour of the root as *response* to *stimulation*. The power of receiving stimulation indicates the possession of special sensitiveness, and its response is to a large extent under the control of the living root. The movements or alterations of growth are purposeful, and lead us to look upon the latter as a living sensitive organism engaged in the task of making the best of its surroundings and varying its behaviour as the surroundings change.

Seeing the very purposeful behaviour of the root we may pause to ask what is the most potent factor in the growth, or what is the determining influence which causes it to penetrate the ground. The fact that stability of position is secured strikes us at once, but it is doubtful if this is the first consideration.

We may dismiss the responses to the stimulation of light and contact. They are accessory to the effort of the plant to come into close relation with the soil, but they by themselves do not minister to any of its needs. The behaviour of the root suggests that it is seeking something which the long experience of the race has shown to be advantageous and which has now become hereditary in the plant. The object of this search is the water which the soil contains, which is present as delicate films surrounding the particles of which it is composed. Inherited experience has shown to the vegetable organism that the soil is the source of water, and its instinctive efforts are directed to the securing of a position leading to an adequate supply.

The stimulus of gravity, therefore, or the perception

of direction, indicates to the root the whereabouts of the water which it needs. The perception of water aids that of direction and under normal conditions the two co-operate. If, however, there be no water in the soil, the inherited instincts of the plant lead it to penetrate even the driest sand.

If the plant is in such a position that the two stimulations do not co-operate, but are antagonistic to each other, the chief instinct of the plant becomes evident, and it can be shown that its great object is the coming into relationship with water rather than with soil.

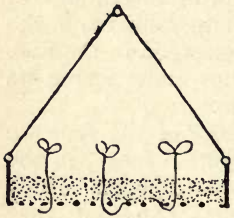

FIG. 10. Hydrotropism. (After Gibson.)

If some seedlings are allowed to grow on a sieve which is covered by a layer of moss they will at the outset put out their roots through the holes of the sieve and grow downwards in a normal way, seeking as their inherited instincts tell them the soil which should normally be situated below them. If the sieve is suspended over a pan of water, so that moist air is below the roots, they keep on growing downwards as if growing into earth. But if the conditions be changed after the roots have attained a length of, say, half an inch, the air below them being made very dry by artificial means, while the moss in the sieve is kept well wetted, the roots soon curve upwards and growing in opposition to gravity turn towards the water (Fig. 10). They appear to recognise that their original instinct is deceiving them and that the true habitat for them is for some reason above and not below them. If after they have established this new direction of growth the conditions be again changed and moisture be restored to the air below them while the moss is allowed to dry, another reversal of the direction of growth takes place and

again the position of the water determines this direction.

The behaviour of the root thus shows it to possess certain tendencies which are based upon inheritance of the accumulated experience of the race to which it belongs, but which are controlled by certain sensitivities which are its own personal possession. These sensitivities are no doubt hereditary also.

The power of appreciating the influence of these various stimulating influences has been found to be confined to a very small region of the root, extending about one-tenth of an inch from the apex. This region, which may be called the *root tip*, may consequently be regarded as a rudimentary sense organ. There is, however, nothing in its structure to mark it off from the region further back. The part receiving the stimulus is not the part which becomes curved in the act of responding. The latter is the region of active growth, where the cells are undergoing elongation. The cells at the tip only retain their sensitiveness for a short time. When new cells are formed in front of them in the process of elongation these are found to be sensitive, and the original ones, passing into the region of active growth, lose the power of appreciating stimulation. There is thus no permanent sense-organ in the root. The protoplasm is sensitive at some particular stage of its development, and, having passed that stage, loses its power of appreciating these stimulating changes.

The way in which the stimulus received at the tip causes a modification of the growth of the cells some little distance farther back is not at present understood. Something in the nature of a nervous impulse is thought to be transmitted from the one region to the other, passing along the delicate threads of protoplasm which extend through the separating walls of the cells and put all the cells in communication with one another.

We noticed in studying certain seedlings, especially

those of the castor oil plant, that the root does not remain single but very speedily begins to give off branches. By this process of branching a very large root system is made possible. The main root of Dicotyledons usually persists and remains longer and stronger than its branches. Such a main root is called a *tap root.* The branches in turn branch and we get roots of the second, third, and higher orders. If we trace the formation of these roots, as we can do by cultivating a seedling in water, or a dilute solution of the necessary mineral compounds, we find that they arise in constant succession as the main root grows, the youngest thus being always nearest the growing point of the main root. Each branch root has the same appearance as the one from which it springs, and similarly bears near its apex a band or zone of root hairs. The branches orginate in the interior of the old root and bore their way outwards. They arise in definite positions, in relations to certain internal structures which will be discussed a little later.

The branches are sensitive to the same stimuli as the main root, but they respond rather differently to the action of gravity. Instead of growing vertically downwards, the first branches stand out nearly at right angles to the main root and persist in growing in this direction. The branches which in their turn they bear do not grow in such definite positions, but extend symmetrically round the one from which they spring. If by accident the main root is killed, its place is taken by one of its strongest branches, which alters its response to gravity and grows vertically downwards.

By this course of development the root system of a plant comes to occupy considerable space in the earth and to fill the interstices of the latter very completely. Two advantages are thus secured: a very firm grip of the soil is secured by the attachment of the root hairs

of the numerous rootlets, spread through so much of the earth, aided very conspicuously by the large network which the branches form; and a very large area of water-covered particles is tapped by the absorbing root hairs the rootlets bear.

As the system gets older, not only is it continually enlarged by the increased branching, but the individual roots and branches increase in girth and press more and more firmly into the soil. They penetrate very deeply and extend laterally very widely, so that with the increasing size of the above-ground portion of the plant a firmer and firmer anchorage is afforded, securing the needed stability.

CHAPTER IV

THE STRUCTURE OF THE ROOT

THE internal structure of the root can be properly understood only when it is studied from the point of view of the work which the root has to do. At its first emergence from the seed its substance is composed of a large number of the vegetable cells which we have described, each a little mass of protoplasm separated from its neighbours by delicate cell walls. They are in close contact with each other at all points and have no cavities in them. The chief difference in the mass is that the external cells at the apex form a kind of cap over the tip of the radicle, so that its actual apex is not exposed. This cap protects the true apex from damage as it penetrates into the soil. When the radicle has begun to elongate changes in the cells are set up. If a longitudinal section of it (Fig. 11) is examined these changes will be seen to separate the young root into roughly three areas. The cap can be seen in front, a short region behind it shows the cells small and actively

dividing, so increasing their number, and a longer part still further back is marked by the enlargement of the cells in all directions, but most notably longitudinally, while their vacuoles are being formed. These regions are known as the root cap, the region of cell division, and the region of cell growth. Little more can be distinguished at this stage.

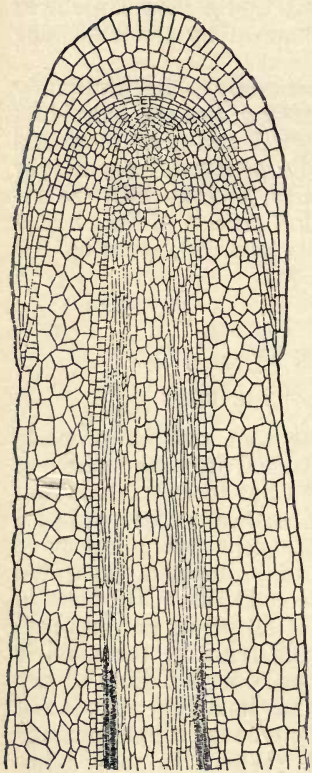

FIG. 11. Longitudinal section of young root. ×20.

A little later, when the external band of root hairs appears, preparation for the discharge of particular duties by the different parts begins to be indicated, while the requirements of the life of the organ involve further adaptations. The first of these is the admission of air to the interior to supply the oxygen all living substance needs to breathe. The commencement of the formation of an aerating mechanism can be traced all through the young embryo, even at this age; as seen in an older root it consists of the splitting of the cells apart from one another at some point of each, frequently at the angles their walls make with each other (Fig. 12). These little splittings make a number of spaces between particular cells, and as growth goes on

these separate spaces become united, so that intercellular passages run among the cells of every region, being of different dimensions in different areas. As we shall see later these passages become open to the exterior in the upper portion of the plant and so enable air to enter and circulate in the interior of the tissues.

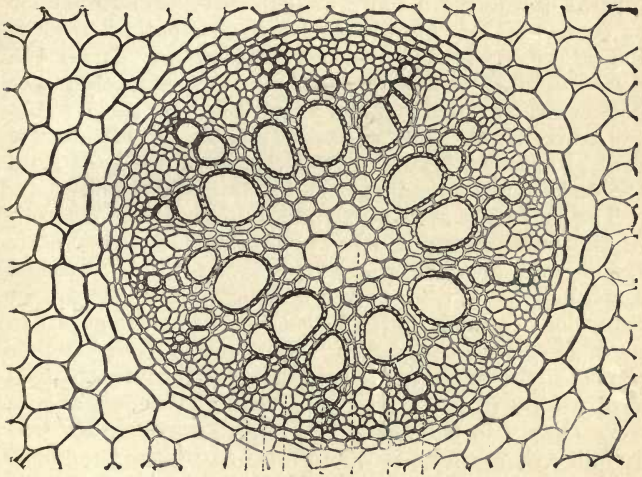

FIG. 12. Section of central part of root. In the outer region the cells are separated in places by the intercellular spaces. *en*, endodermis; *pe*, pericycle; *ph*, phloëm strand; *p*, pith; *x*, xylem strand; *px*, protoxylem. ×100. (After Kny.)

A longitudinal section of the root taken at this age will show that beside the longitudinal areas or regions already remarked the internal tissue is beginning to be differentiated in another direction. The section of the root is almost conical, but the apex of the cone can be divided into three layers, each of which is continued backwards along the axis. At the apex each layer can

be recognised in the zone of cell division. The cells of these layers can divide and they are called in consequence *meristematic* layers. The outermost, which is known as the dermatogen, forms the root cap, and extending backwards gives rise also to the outermost layer of the root from which the root hairs grow. The central one forms a more or less well-marked cylinder or core, which is known in the meristematic region as the *plerome*, while the intermediate one is called the *periblem*, and forms the part of the root that lies between the central cylinder and the external layer. As we trace these further backwards we find that the central cylinder becomes very clearly marked off from the rest by a peculiar layer called the *endodermis*.

The root hairs are long slender outgrowths of the cells of the outer layer, which when past the meristematic region is known as the *piliferous layer*, or *epiblema*. Each hair has a thin wall of cellulose, which is brought into close contact with particles of soil as it grows in among them. On coming into contact with these particles the outer layers of its walls become changed into a kind of mucilage, which makes the hair adhere very closely to the soil. The film of water which surrounds the particles is then absorbed by the root hair. As there are enormous numbers of these hairs on the young root, there is soon a great increase in the water which the root contains. This water passes on from the hairs into the second region of the root, now called *cortex* instead of periblem, and gradually makes its cells extremely swollen or *turgid* thereby.

The special mechanism for carrying this water from the root to the upper parts of the plant is by this time beginning to appear. It lies in the central region, now partly shut off from the rest by the endodermis. Here the growth of the cells is such as to cause them to become elongated. Certain special areas of these

elongated cells form a definite number of columns of cells which can be traced separately upwards. They are fitted especially to transport water by changes in the constitution of their cell walls, which become gradually changed from cellulose to lignin, the latter enabling water to pass through it in all directions with great ease. At the same time the horizontal walls of

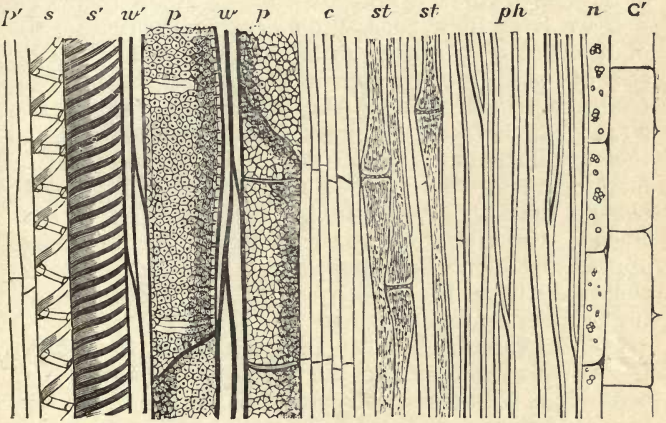

FIG. 13. Longitudinal section through a vascular bundle of a stem. *s*, *s'*, *p*, *p*, different types of wood vessel; *w*, wood fibres; *st*, sieve tubes; *ph*, bast fibres; *p'*, pith; *c*, cambium.

these cells in great part disappear, so that the columns of cells become changed into hollow tubes, or *vessels*, while their side walls are irregularly thickened by the deposit of more cell-wall substance upon them in particular areas. On account of the presence of these vessels, the collections are known as *vascular strands* or *vascular bundles* (Fig. 13). In the root they are composed entirely of lignified cells and are therefore called *wood* or *xylem* bundles, to distinguish them from other vascular strands lying near them. The number of these

strands varies in different roots; it is very common to find four, but two is not an infrequent number. They may extend completely to the centre and all unite there to form a solid cylinder. If the number is large they generally fuse together before extending so far, leaving a small-celled column as a core. This is known as a *pith*. In form the bundles are wedge-shaped, the apex of the wedge pointing outwards.

If we trace these conducting strands towards the tip of the root they can be distinguished among the soft cells of the plerome by their narrow diameters and their tendency to elongation. The area of each embryonic strand can be seen distinctly in a transverse section, their small size and a certain density of their protoplasm marking them off from their neighbours. The gradual change from these cells to the mature forms can be traced; the alteration of the wall and its thickening appear first along the outer edge of the wedge, known consequently as the *protoxylem*, and extending thence towards the centre of the root.

If these vascular bundles are traced along the root in the direction opposite to the tip they are seen to be continuous with similar structures in the stem. In this way a path is made throughout the plant for the transport of the water after its absorption.

These strands are chiefly concerned with the function of the root. Others which also are traceable throughout the plant can be seen to lie one between each pair of them in the central cylinder. These are chiefly concerned in the nutrition of the root. They are equally well defined and lie side by side with the wood strands, separated from them by a few packing cells. They differ in texture, their walls remaining cellulose. They are known as *bast* or *phloem*; and are made up of vessels known as *sieve tubes* from their terminal walls being somewhat thickened and perforated

by a number of holes, so that their protoplasm is continuous (Fig. 13). With the sieve tubes are a certain number of slightly elongated cells of the ordinary type.

The bast and wood strands are thus seen to occupy, with a little supporting tissue, almost the whole central cylinder of the root (Fig. 14). There is always an outer

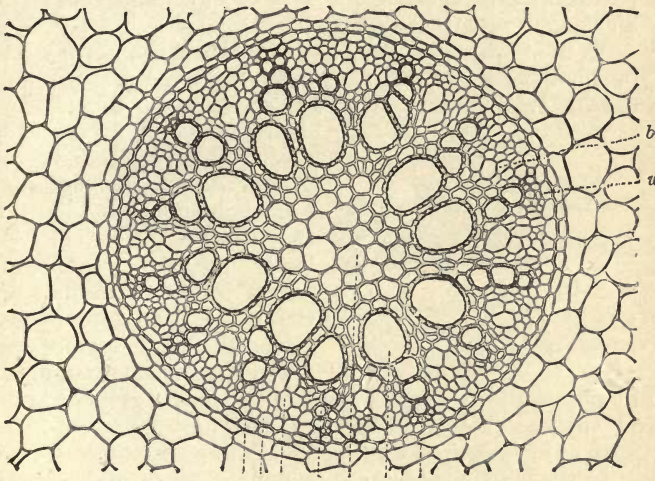

FIG. 14. Section of central part of root. *b*, bast strands; *w*, wood bundles. ×100. (After Kny.)

continuous sheath over the whole, one cell thick as a rule, which is called the *pericycle*. Outside the pericycle comes the endodermis.

The endodermis forms a sheath, one cell thick, round the central cylinder. Its walls in some cases become uniformly thickened and lignified. In others the outer and inner walls remain thin, while the side walls become changed in a different way. The cellulose is replaced by another material which resists the passage

of water through it, so that the water of the cortex can pass directly to the wood strands, but cannot pass from one endodermal cell to another, being prevented by bands of a cuticularised substance that pass round the radial walls (Fig. 15). By their interlocking together they make the endodermis separate the intercellular passages of the cortex from those of the cylinder, so that air cannot penetrate directly to the latter.

As the root grows older and larger and the upper part or shoot system of the plant develops to a corresponding extent, this primary structure becomes insufficient for its requirements. They call for a greater amount of conducting tissue as the branches and leaves of the shoot multiply, for all the latter need a supply of water. The stability of the whole structure needs strengthening, in view of the greater size being acquired above ground. There is, as we have seen, a great growth in thickness of the root and the development of a system of branches, each behaving like the parent root.

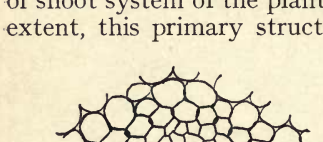

FIG. 15. Part of endodermis of young root, with underlying pericycle.

In the stage we have examined the young root shows no provision for this increase of thickness. It can take place only by the formation of new cells, and such formation is not going on except at the apical meristem. A new departure has accordingly to be made (Fig. 16). It begins by a curved band of cells of the supporting tissue lying in front of each strand of bast becoming meristematic, beginning to divide by walls which are parallel in direction with the circumference of the root. These tangential divisions cause the formation of several rows of cells, one of which, the nearest to the bast, retains the power of division and is called *cambium*.

The newly formed cells become converted into wood, so that a strand of wood, called secondary wood, is formed inside each bast bundle. The cambium layer

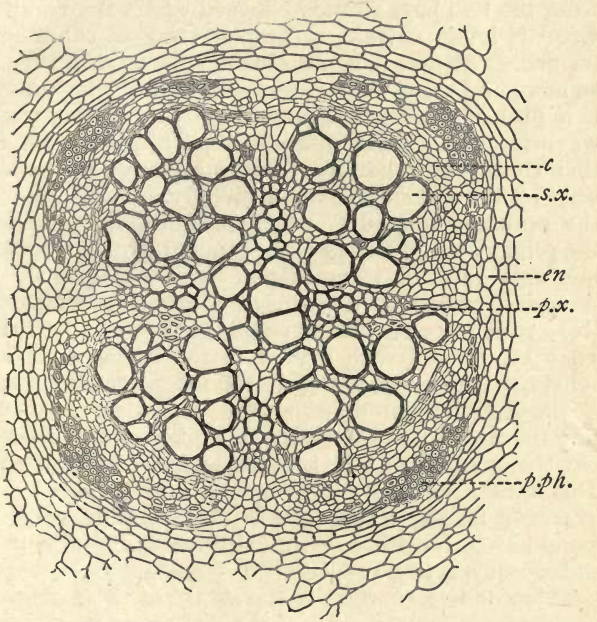

FIG. 16. Thickening of root; *px*, primary wood; *sx*, secondary wood; *c*, cambium; *en*, endodermis. ×80. (After Kny.)

extends laterally round the bast bundle, so that it tends to pass up towards the outer edge of the wood bundle on each side. By the time a little mass of wood has thus been formed between each bast strand and the centre of the root, the cells of the pericycle outside the wood bundles divide by similar tangential walls, so

that the pericycle at these points becomes several cells thick. The innermost of these cells, lying in contact with the protoxylem, become cambium, and soon extend to unite the two bands of cambium approaching them from the two bast strands between which the bundle of wood is lying, so that a complete ring of cambium is formed. At first it is necessarily sinuous or wavy, but as more and more wood is formed inside the bast masses it is pushed further and further outwards there, till the waviness of the ring disappears. This cambium ring then continues to add more and more wood in the same way to the secondary wood already formed. Behind the protoxylem groups, which form the outer edge of the primary wood bundles, no secondary wood is formed, but only rows of thin-walled cells; consequently the secondary wood is divided into separate masses by these rows of cells, which are known as medullary rays. They are formed with a view to the transport of food substances from the bast into the interior of the wood.

The cambium produces a little secondary bast outside the ring in the same way as it forms wood inside it, but the quantity of bast is much less than that of wood. This is natural, as the bast has only to provide a path of transit for the actual food of the root cells, while the wood has to furnish a continually increasing amount of water-transporting tissue.

This woody formation in the centre of the root is disposed very advantageously for maintaining its stability. A structure with a hard central core is the most suitable to resist such a vertical pull as would cause uprooting. This vertical pull is continually being made by the movement of the storm-tossed upper region of such a structure as a tree.

The young root as it increases in thickness in the soil encounters two dangers, one internal, the other external. The process of thickening compresses very severely

its more external layers and in time ruptures them. The pressure of wet soil against its epiblema is not unlikely to set up decay. The cortical tissues and the epiblema are therefore inadequate to protect the gradually thickening central cylinder. But these difficulties become obviated as the growth proceeds. By the time the central cylinder has become only slightly thickened the zone of the root hairs has been removed to some distance in advance, by the continuous elongation of the root. The cortex of the thickened part is consequently not supplied with water as before, and ceases to play its original part in transporting the water upwards. The hairs having disappeared from that region too, the epiblema has not its first importance there. The pressure of the gradually increasing girth stimulates the cells of the pericycle and they again show the power of increasing by tangential divisions. The pericycle becomes uniformly several cells thick, one layer of which remains meristematic. It cuts off repeatedly bands or shells of cells which remain very regular in shape, appearing in transverse sections like rows of bricks. The outermost ones lose their contents and their walls are transformed into suberin, a substance closely resembling the cuticularised material of the endodermis. This band of cells forms what is known as a *cork* layer. It extends completely round the root and forms a strongly protecting sheath. It is perforated here and there by little rounded masses of cells loosely arranged so that air can pass between them. These are known as *lenticels;* they serve to admit air to the interior of the root. It is quite impervious to water except at these spots, and hence preserves the root from loss of water by outward leakage. The cells of the cortex and epiblema may now rot away without causing any damage to the root. The latter acquires, in fact, a fresh exterior of a more resistant and permanent character than the

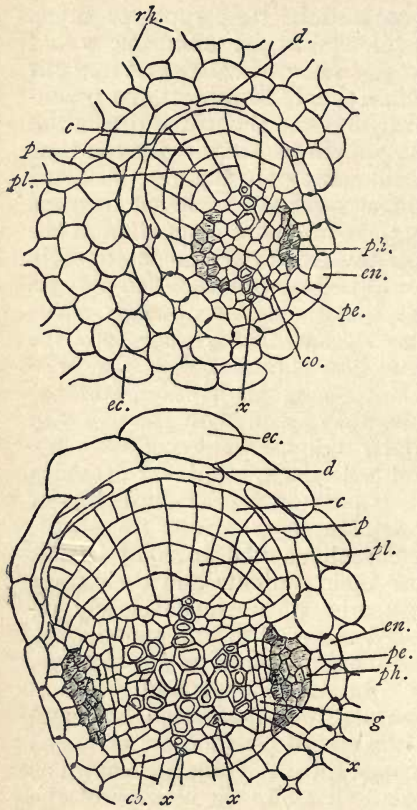

FIG. 17. Transverse section of root to show a rootlet at two stages of development. *rh*, root hairs; *ec*, cortex; *d*, cells in process of absorption; *en*, endodermis; *pe*, pericycle; *co*, conjunctive tissue; *ph*, bast; *g*, cambium; *x*, wood; *c*, dermatogen of rootlet; *p*, its periblem; *pl*, its plerome. (After Scott.)

original one. This corky formation continues as long as the root lives and adapts itself to its increasing girth. Its outer part is composed of dead cells, and together with the remains of the layers originally outside it, constitutes the *bark* of the root. The cortex and epiblema continue for a very short time, so that in an old root the bark consists of pericycle tissue and layers of cork.

We must again return to the young root to trace the manner of formation of its branches. The latter originate when it is quite young, as we have seen already. They arise in the pericycle, in very many cases opposite to the protoxylem of each wood bundle, generally before the strands are lignified throughout. There are consequently usually as

many rows of lateral roots as there are wood strands. A little group of the cells become marked out by becoming meristematic, and dividing chiefly by tangential walls, so that soon a little mass seems to be growing outwards. It can shortly afterwards be seen to have a central plerome covered by a periblem and dermatogen, which behave just like those of the parent root. The cells of the cortex which lie in front of the new root branch are gradually digested and eaten by the latter as it grows outwards and finally penetrates to the exterior (Fig. 17).

The cells of the root cap are continually being worn away by contact with the soil. The cap is added to all the while by the dermatogen behind it.

CHAPTER V

THE CHARACTERISTIC FEATURES OF THE SHOOT

THE work which falls upon the shoot portion of the plant is very different from that discharged by the roots, being very largely the construction of the organic substance which serves as food, not only for the plant itself but for the world in general. To understand this construction we must consider the absorption of carbon dioxide, the utilisation of certain amounts of the water and mineral constituents furnished by the roots, and the evaporation of the surplus water. The work involves certain minor or subordinate duties connected with the distribution of the food after its formation.

The important questions of the breathing of the plant and the maintenance of a suitable temperature in its different parts must also engage our attention.

The form and composition of the shoot need careful study from these points of view, but these are not all. The relation of its structure, internal as well as external,

to its stationary position, and the difficulties and dangers which the latter presents, must be considered. The adaptations which it shows and the changes of climate which it meets are of great importance. Finally, we have the relation of the shoot system to the processes of reproduction.

When the young shoot has emerged from the seed and made its way into the air in the ways already described, the bent or hooked form gradually changes till an upright position is attained. We have already examined the behaviour of the young root, noting its perception of direction and its modification of its growth if necessary, till it can make its way vertically downwards. The same appreciation of direction is exhibited by the young shoot and its behaviour is very similar, with the important difference, however, that it seeks the light and air and hence grows vertically upwards. We cannot explain this difference except by recognising the purposeful character of its response to the influence of gravity. There is no difference in the growing cells, so far as we can see, for they have all practically the same structure whether they are in root or shoot. We see in this behaviour really a living organism trying in a limited way to make the best of the circumstances in which it finds itself. As we continue to study it we shall be able to ascertain that it possesses the same sensitivities and powers of response to changes in its surroundings that we have found exhibited by the root.

The growth of the shoot, however, is a much more complicated process than that of the root, in consequence of its more manifold duties, which have called for a more complicated structure.

The young plumule when it has emerged from the seed coats consists of a very delicate axis, at the apex of which a number of minute outgrowths are to be seen. These are folded in various ways, the outermost covering

those internal to them. Their number is not uniform, nor is their method of folding, nor their arrangement, but they all arch over the apex of the shoot. The latter does not bear any protective cap, such as is seen over the root. It is a delicate conical tip, which bears its outgrowths in regular succession, the latter being continually developed by the apex as it elongates, so that the youngest are always nearest to the tip.

These outgrowths are borne upon the axis at definite points, which show a remarkable difference of behaviour from the spaces between them, in that they do not elongate during the processes of growth. All the growth in length is carried out by these spaces. The points at which the outgrowths are borne are called *nodes*, the spaces between them *internodes*.

The behaviour of these parts can be studied advantageously on a shoot a little older than the plumule.

It is well to select a tree of some few years' growth and to examine some of the ultimate endings of its branches. If from such a tree in the early spring we take a twig we shall be able to observe that during the previous summer its internodes elongated, causing the outgrowths to be separated from each other by some little distance. The year's growth may have caused the shoot to become perhaps three or four inches long. If we examine the nodes closely we shall find that between the original outgrowths and the axis certain small knob-like bodies occur, almost hidden between the others. These several parts can always be observed with greater or less facility on all shoots. The axis is called the *stem*, the first-formed outgrowths are the *leaves*, and the little knob-like bodies between the two are known as *buds*. The angle between the stem and its leaf in which the bud arises is the *axil of the leaf*. The apex of the stem will be seen in the spring to exhibit also the form of a bud, rather larger than the lateral ones in the axils

of the leaves. The plumule is really the first bud of the seedling, and it shows fundamentally the same structure as the others appearing later on the stem.

As the seasons of the year in our climate render growth intermittent, confined to little more than half the time, and as the growing shoots are exposed to very unfavourable conditions during the remainder, it is easy to understand that special precautions are called for,

FIG. 18. Buds of lilac. A, shows the external appearance; B, a slightly magnified section; C, the bud-scales are reflexed and the leafy shoot has begun to elongate. (After Marshall Ward.)

that they may develop. If we cut a longitudinal section through one of these buds in the spring before growth is resumed we shall find evidence of such (Fig. 18 B). The delicate growing cone in the centre will be found to be surrounded by a varying number of leaves, each of which arches over it and is in turn arched over by the next one external to it. The most internal ones are extremely delicate and almost unformed, while the cone itself if magnified will be seen in many cases to bear upon its surface small swellings which indicate that other leaves are in course of formation there. Over

these delicate leaves are others more sturdy, while the exterior ones are frequently quite dry and hard and in many cases covered over by a sticky substance. Some of those in the interior are in many cases covered with thick coatings of hairs, forming a downy pad of material calculated by its non-conductivity to keep out the cold.

If the bud is small, it will be found to contain only a few leaves, perhaps only two or three; even in this case, however, the general arrangements are the same.

If we compare the apices of stem and root, we see how the surroundings in each case have influenced the structure. The root apex is specially protected against damage from contact with hard or rough materials while penetrating through the soil; the stem is exposed to no such danger, but shows a careful protection from frost and wet, and undue evaporation.

The young leaves are thus merely flattened boat-shaped expansions curling over the apex of the stem. Later, when their protective powers are no longer called for, their adult forms are assumed.

The leaves bring about their curving over the apex of the stem in the bud by an irregularity of growth. When the little swelling first appears on the growing cone it is itself rounded or conical; it soon becomes laterally flattened and for a time, so long as it is in the bud, its under surface grows faster than its upper one, so that it is made to curve forwards. When it escapes from the bud later it reverses this distribution of growth and grows more rapidly on its upper face, so becoming flat.

Buds always terminate the ends of normal growing shoots; indeed the bud-form is always assumed by the apex of the shoot as soon as its growth is suspended by unfavourable conditions. The buds which appear in the axils of the leaves lower down on the stem are the commencements of the secondary shoots or branches, which will elongate in due course.

In many cases the bud is the foreshadowing of the growth of the stem or branch of the next year. It has been formed by the shoot as its last effort for the year, and its development during the succeeding year will only involve the elongation of the internodes, the assumption of the adult forms of the leaves, and the preparation of the buds for the year following. In other cases it is not so simple. During the growing period more leaves will be produced than the bud in its resting state exhibits, and growth will be prolonged accordingly. But even in these cases as soon as growth in length stops, the development of another terminal bud with its potentialities can be noticed.

The growth of the shoot thus shows considerable differences from that of the root. In the case of the latter it is not at all easy to say what are the limits of the year's elongation, while in that of the shoot they may be fairly accurately determined.

When the next growing season sets in, the bud begins to swell owing to the upward pressure of the elongating axis. The outer leaves are loosened and pressed apart, so that the bud bursts open at the apex. When the external leaves are hard scales they are generally cast off entirely, and the internal leaves emerge. The elongation of the several internodes rapidly follows and the shoot takes on its proper form.

As this change proceeds certain other facts can be determined. The external scales have no buds in their axils, nor do all the leaves develop into foliage leaves. The external ones, and often some just internal to them, do not change their form, and frequently only persist for a short time, soon falling away. All these are classed together as *bud-scales;* they really represent only the bases of leaves (Fig. 18 C).

As growth goes on other differences appear. The internodes between the bud-scales do not elongate, so

that while the scales persist the young shoot seems surrounded by a number of small leaves at its base (Fig. 18 C). When the bud-scales fall off, they leave the base of the shoot surrounded by scars, which mark the places of their original attachment. At the close of growth on the onset of winter, the shoot, now become what is technically called a *twig* (Fig. 19), shows these scars closely placed together round its base. In the winter it is easy to recognise the amount of growth of a twig during the preceding year, by noting the distance between this collection of scars and the apex. In an older twig or young branch several such collections of scars can be detected, and so the limits of each year's growth can be easily ascertained.

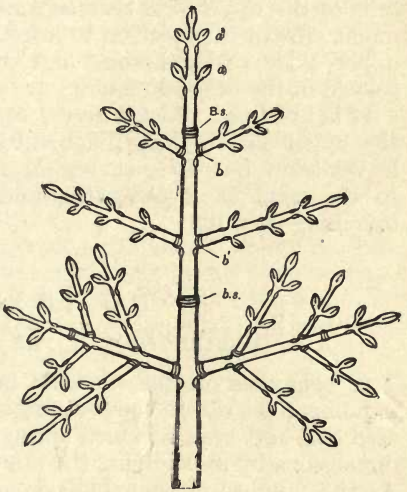

FIG. 19. Twig of 3 years' growth. *bs*, scars of bud-scales of each year. The twig shows racemose branching. (After Ward.)

With the opening of the bud and the expansion of its leaves as its stem elongates we can trace the sensitiveness of the shoot to the various influences that surround it. We have pointed out the response its axis makes to the influence of gravity and lateral light. We have also incidentally mentioned the change of the curvature of the leaves which sets in as soon as the bud opens. The change is a response to the access of light

which accompanies this opening. The water in the cells of the leaf was in the early stages of development distributed mainly to those of the under side, making them most turgid and causing them to grow most freely. The access of light disturbs this relationship and the cells of the upper side become most turgid; the consequent growth causes them to lose the concavity of their upper sides; they become flat or sometimes slightly curved in the other direction.

If light is not allowed access to them this growth of the upper side is very much interfered with, and the leaves show but little change of curvature, lying close to the stem as it elongates, and in some cases not becoming even flat.

CHAPTER VI

THE CONSTRUCTION OF THE SHOOT SYSTEM

THE behaviour of the plumule in elongating and expanding gives rise to the primary shoot. Every successive bud and branch which spring from it increases its dimensions by multiplying the number of twigs it bears. As the number of such buds upon each twig is fairly large, we see that the young branches increase in a kind of geometrical progression, causing the formation of a large shoot system, which constitutes the body of a shrub or the head of a tree. We must next study the construction of such a head.

To understand it we must inquire what are the purposes for which it exists, and what are the dangers against which it must protect itself.

We have already drawn attention to the fact that the functions of the root and the shoot are fundamentally different. That being so, it seems clear that the mode of arrangement of the parts of the one need form no

rule for the other. There is nevertheless a general agreement between the two, though careful observation shows that similarity of arrangement subserves very different purposes. The arrangements of the shoot all bear a certain relationship to life in air and its consequent requirements, and show further a co-ordination with the needs which are cared for by the roots.

We have seen that one of the primary objects of the latter is to secure a firm anchorage for the plant that it may be able to maintain its erect position. The development of a large head or upper part makes against such anchorage, by offering a large area to the pressure of wind and the beating of rain—forces likely to lead to uprooting from the soil.

We may ask why such a risk should be undertaken—why the sub-aerial portion of the plant need attain the large dimensions it possesses. What are the advantages which are afforded by a widespreading head rearing itself into the air? Are they commensurate with the risk, and what are the precautions which protect the plant in face of the dangers it involves?

In seeking answers to these questions we must look a little more closely at the chief features of the upper portions of the shoot system. We soon see that one of the objects secured by the method of development which it follows is the great amount of surface in proportion to bulk which the shoot presents. The twigs are thin, the leaves flat. We have indeed, as we have in the root, and as we notice in the case of the large seaweeds, the bringing of the structure of the plant into relationship with as large a portion of the environment as possible. Here is clearly an indication or suggestion of an interchange of material between the two.

We have already assumed that there is such an interchange, and may now examine more closely its nature. A few simple observations will enable us to prove it.

Let us remove a twig with its expanded leaves to a confined space, so that we examine the conditions of the air around it to see what changes, if any, take place. Let us shut it up in a well-dried bottle and keep it at its accustomed temperature. We shall find after a short time that the sides of the bottle become bedewed with moisture, and a little later we shall see that the leaves upon the twig and at least its upper part become wilted and drooping. Part of the work of the shoot is clearly to exhale watery vapour from its surface.

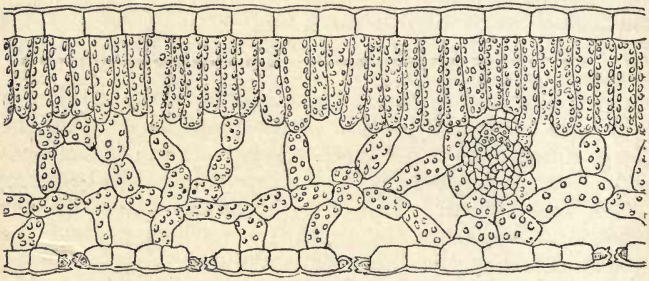

FIG. 20. Section of leaf showing intercellular spaces and stomata. The cells contain chloroplasts. ×80.

If careful measurements are made of the total water a plant gives off, it is found to be very considerable in amount, and to be given off during the whole of the day in quantities varying with the changing conditions surrounding the plant. The structure of the leaf, to which we must give later some careful attention, shows us that the intercellular spaces which we observed in the body of the root exist in even greater degree in the leaf (Fig. 20) and yield an evaporating surface much larger than the external surface of the twigs and leaves. These internal channels communicate with the exterior through small openings in the limiting membrane of the

leaves and the more delicate parts of the twig. These openings, which are known as *stomata*, are themselves co-ordinated with the regulation of this exhalation of vapour, the width of the opening being capable of variation according to different conditions. We must associate the evaporation of so much vapour by the leaves with the very large absorption of water we observed in the root, and we can see that the structure of the leaf is as well adapted to evaporation as that of the root is to absorption. Further structural adaptations to this maintenance of a stream of water through the plant will become evident later, but in the meantime we can see in the features already alluded to a definite relation to this particular interchange between the plant and its surroundings or environment.

Still pursuing our inquiry, we may notice that while the general colour of the shoot is green, the depth of the green tint is not uniform. The flattened parts or leaves are of a brighter green than the cylindrical axes, and in general it soon appears that the more exposed any part of the shoot is in its young and most delicate condition, the more prominent the green colour becomes. We have consequently a suggestion of some co-ordination between exposure and colour. Comparing two shoots growing in different places we can soon associate the optimum brightness with the best illumination, and we are led to infer that one reason for the flatness of certain parts of the shoot is the desirability of exposing as much of their surface as possible to light.

We have already called attention to the fact that the greater part of the plant's food is manufactured in the leaves, and that the green colouring matter—chlorophyll—is chiefly concerned in making it. The chlorophyll is not diffused throughout the living substance, but is confined to a number of small ovoid bodies which are embedded in it, and these green bodies are placed very

little below the surface of the leaves, being thus covered only by a thin transparent layer of cells. The distribution of these green bodies, which are known as *chloroplasts*, so bears a very definite relation to the incidence of the light, and suggests to us that while one duty of the leaf is to exhale watery vapour, another is to secure the illumination of a definite part of its mechanism, which is concerned with the most intimate questions of nutrition.

As the two functions thus suggested are found upon further inquiry to be intimately bound up with the well-being of the plant, we must examine them a little more closely before looking for the ways in which they influence the form and position of the shoot system.

There are two reasons for the copious evaporation of water which we have pointed out. The first is connected with the problem of feeding, as we noticed in our introductory chapter. Certain constituents, either entering into the composition of the food itself or necessary factors in its construction, are only to be found in the soil and are procured therefrom by the roots. These compounds are absorbed from the soil in solution in the water entering the root hairs, and the solutions are necessarily very dilute to facilitate their passage through the living substance of the hairs. As with a rapidly-growing plant continuously increasing quantities of these substances are needed for nutritive purposes, it follows that large quantities of the solution must be absorbed. In the plant these mineral compounds are taken from the water, and the great bulk of the latter is evaporated into the intercellular passages and the vapour subsequently passed out of the stomata. Hence, speaking broadly, the more water that is taken up and subsequently evaporated, the more mineral matter is secured for the use of the organism.

But there is another and equally important function

that this evaporation discharges. In the time of sunshine a great deal of the sun's energy in the form of heat and light is falling on the plant. It has been computed that the amount is so great that it would raise its temperature to such a dangerous extent that if no counter-influence were at work it must speedily perish. Now the evaporation of water always requires the expenditure of a considerable amount of heat, and we find that the greater part of the heat reaching the plant from the sun is devoted to the vaporisation of the water in the intercellular passages of the leaves and other parts. The normal temperature of the plant is thus maintained in the face of the enormous absorption of solar heat which its exposed and often unprotected position renders inevitable.

The study of the behaviour of the chloroplasts shows us that their position is definitely associated with the duty which we have attributed to them. Not only is their colour dependent on their exposure to light, but the part they play in the construction of food is equally related to the illumination they receive. We have already spoken of the work done by the chloroplasts, and have seen that they construct organic food in the form of sugar and similar compounds from the carbon dioxide of the air, together with a portion of the water supplied them by the root. Carbon dioxide is present in very small proportion in the air, only some 3 or 4 parts in 10,000. The construction of food from such antecedents is only possible in the presence of light; two things therefore must be secured—a wide surface and preferably a copiously subdivided one, to bring as much air as possible into contact with it, and as complete an exposure as possible of the chloroplasts to light to enable the construction of the sugar to go on.

The form and disposition of the shoot system must be regarded from the point of view of these require-

ments. True, at first sight they seem a little antagonistic to other needs. The evaporation of the water and the illumination of the chloroplasts demand a large and increasing shoot-body, but its increase in size brings with it a distinct danger to the stability which we have seen is one of the first necessities of the plant as a whole. The reconciling of these demands must add to the interest with which we study the form and distribution of the members of the shoot system.

We have seen that the axis of the latter is very much subdivided, the ultimate divisions, the branches, tapering to points, in some cases extremely gradually, in others more abruptly. These cylindrical or conical divisions bear a number of flattened organs, the leaves, which are usually attached to the axis by flexible stalks or particles. We can now see the reason for this subdivided conformation. It secures *strength* by the cylindrical form of the twigs, *surface* by the flattened form of the leaves. The winds can blow freely through the mass of twigs, while the long leaf stalks allow of sufficient displacement of the flattened parts when the pressure of the wind is brought to bear upon them. Moreover, the parts concerned are all extremely flexible and elastic, so that they can yield to pressure and regain their positions as soon as it is removed.

The form of the shoot system of a plant will depend upon the manner of its branching, and the number, size, and arrangement of the leaves its branches bear.

The branching will be affected by two main factors: firstly, the number of branches produced at a node; secondly, the relative degree of growth of each main branch and those to which it gives rise.

The first of these does not show as much variety as might be expected. Usually one branch, not infrequently two, appear at a node, but seldom more.

The second factor, however, plays a much more

prominent part in the construction of the head. If the first axis grows more vigorously than its branches—a behaviour we found to lead to the formation of a tap root in the root system—and if each of the branches in turn is longer and stronger than those arising from it, the ultimate form of the head is pyramidal, for the successive branches arise nearer and nearer to the apex, and so long as the growth is regular the lowest will be generally the most widespreading. This is true of the series of branches which each of them bears. This type of branching is said to be *indefinite* or *racemose* (Fig. 19), and it is illustrated by such trees as the spruce fir.

If, on the other hand, the growth of each axis or branch is soon checked and so its development becomes exceeded by the growth of the daughter-axes to which it gives rise, the head will be sub-globular or rounded. The exact shape, however, will largely depend on the number of branches springing from below the apex of each in turn, for these all arise at the same node. They are therefore on the same level, and do not grow in what is called *acropetal succession*, as in the first case. A very common form is that in which each branch is solitary. This form of branching is called *definite* or *cymose*. Examples are afforded by the elms, oaks, and many other forest trees (Fig. 21).

Another factor in the shape which the branching helps to give to the shoot system is the non-development of some of the buds. We have seen that a bud is produced in the axil of every foliage leaf. It often happens, however, that a twig cannot adequately feed all the buds it bears. Hence some perish and others remain dormant for some time, circumstances which cause a good deal of irregularity.

Before we study the influence of the arrangement of the leaves upon the form of the shoot and the shoot system we must look a little more closely at the peculi-

arities of their flattened form. We have seen wherein lie its advantages, but we must consider also the difficulties and even dangers which it involves. Difficulties arise from the certainty that the leaves must encounter rough weather in the course of the year. Rain may soak them through, wind may tear them apart, or even strip them from the twigs. How are these perils met?

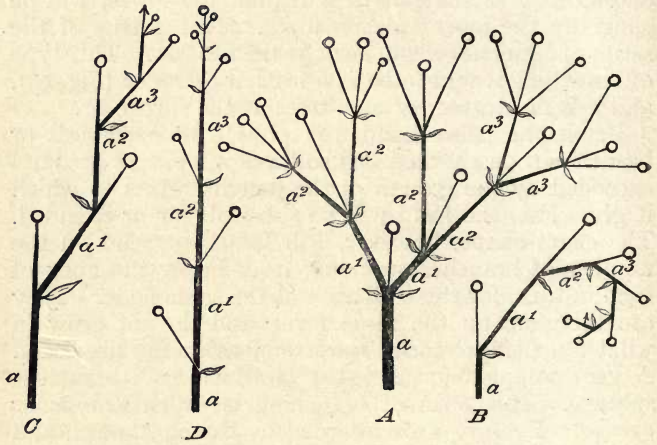

FIG. 21. Diagram of forms of cymose branching.

There are two reasons why rain falling upon them does not affect them seriously for a long time. Generally the shape of each is such that there is a longitudinal groove all along its upper surface, running from apex to base in the centre of the flattened blades. This conducts the water away as fast as it falls upon the leaf, either towards the apex or towards the base. In the latter case the groove is continued along the leaf stalk so that the water is taken to the ground. The second reason is that the outer layers of the walls of the cells

of the upper surface become almost impermeable by water. It is only after long soaking, therefore, that any can find entrance.

The danger from wind is perhaps greater than that from rain. The leaf-blade, however, though delicate and thin, is nevertheless very strong and not easily torn. Running through it are the ultimate endings of the vascular strands we have already noted in the root, the conducting tissue (Fig. 22). These strands form the so-called *veins* of the leaf and they constitute a network of very tough fibrous bands upon which the delicate tearable tissue is supported. They generally strengthen particularly the margins and the apex of the leaf-blade and protect it from being torn. The blade, therefore, when acted on by wind is seldom either bent or curled, but is made to play as a single rigid piece moving up and down without losing its flatness for a moment.

FIG. 22. Venation of leaf.

The danger of stripping from the twig is dealt with differently. When the plant is of a sturdy, rigid habit, the leaves are usually attached to the stem very strongly, and are bent upwards so that the direction of the wind must drive them towards the stem, and its force cannot be felt between the latter and the leaf's upper surface. More frequently, however, we find that the blade of the leaf is attached to the twig by means of a tough, flexible stalk, capable of movement in almost every direction on its point of attachment. The elasticity is so great and so readily called into play that with even the lightest breezes the leaves of most trees are seen to swing to and fro with the greatest freedom.

The form of the head of the tree is influenced by the

shape as well as the arrangement of the leaves. Usually leaves consist of three regions, a flattened part or blade, a leaf-stalk or petiole, and a leaf base by which it is attached to the stem. If we regard it as an outgrowth from the stem, we find that it assumes its flattened form by developing a wing on each side, the outgrowth itself also becoming flat. If the outgrowth branches and only its branches develop wings we have what is commonly termed a *compound* leaf (Fig. 23).

FIG. 23. Compound leaf.

The leaf-stalk is the lower part of the axis of the leaf and it is continued forwards to the tip, the part which has become winged being called the *mid-rib*. In some cases the whole of the axis of the leaf becomes winged. The leaf is said then to be sessile or to have no stalk. At the base of the leaf are very frequently two small outgrowths, of the nature of leaf branches. These are known as *stipules*. They vary a good deal in shape and size.

The object aimed at in the distribution of leaves on a tree is the covering of the framework of its head as completely as possible by a thin curtain of leaves, as free from unoccupied gaps as possible; the leaves themselves must be so arranged that little shading of one part by another shall occur. If we stand under a tree and look up through its branches we find the leaves are not distributed all about the interior of the space occupied by the boughs and branches; they are seen to be a more or less complete covering to the head. In a humbler type, such as a thistle or a sunflower, the leaves overlap very little, so that practically the whole leaf-surface is exposed to the light during at any rate some part of the day.

The leaves are arranged in various ways upon the

stem, but always occur in vertical or nearly vertical rows. Sometimes only one leaf originates at each node, sometimes two, or occasionally more. When only one occurs the leaves are found to be arranged *spirally* or *alternately* up the stem. When more than one there is said to be a *whorl* of leaves at each node. Frequently the whorl consists of two leaves only. Successive whorls, whatever the number of leaves, have their separate leaves placed opposite the spaces between the leaves of the whorls above and below them.

The number of the vertical rows is correlated with the shape and size of the leaves which compose them. Leaves with very broad bases, often indented, and tapering fairly rapidly to a pointed apex, known technically as *ovate* or *cordate* leaves, generally occur opposite to one another on the stem, there being only two rows. Sometimes they have short stalks, sometimes none. When the leaf has its broadest part near the middle and tapers to both apex and base it is termed an *oval* or *elliptical* leaf; such are generally arranged in three rows. When still narrower, becoming what are known as *lanceolate* leaves, the number of rows increases to five or eight. Still narrower leaves occur in greater numbers of ranks still. We see thus a co-ordination between the shapes and dimensions of the leaves and their mode of attachment to the stem, just such a co-ordination as we should expect when we remember the disadvantages which would arise from a crowding together of large ovate leaves in several ranks, or the sparse scattering of linear or narrow leaves in few rows.

When we study in this way the shoot systems of different plants we find them to be in harmony with their surroundings as fully as are the root systems. The surroundings influence the plant very forcibly while it is developing, and many of the results of its development can only be understood by observing that they are

essentially purposeful. The only mode of securing this adjustment with the environment which is possible is that of regulating its growth.

During the early development and growth the plant exhibits in its shoots as in its roots powers of purposeful response to certain features of the environment which it is capable of appreciating. If we examine the plumule or young bud of the seedling as soon as it begins to grow, we shall notice the same perception of direction as we observed in the root. As the latter would persist in growing downwards, curving itself if its apex pointed in any other direction, so the shoot persists in growing upwards. The sensitive part is not so easy to localise as in the root, but careful experiments made on various plants have proved that the perceptive part of the shoot is the tip and that the sensitive zone does not extend far downwards. The response to the stimulus is brought about in the same way in the two cases, viz., by a modification of the growth, and it is clearly purposeful, to plant the root in the earth and the shoot in the air. There is a close resemblance again in their behaviour between the primary branches of the stem and root. None of them grows in the same direction as the axis from which it springs, but usually they stretch out nearly at right angles to it. This is a response to the stimulation of gravitation in both.

Another factor which is of much greater importance in the case of the shoot than in that of the root is the incidence of lateral light, which helps to determine the position of the branches as well as of the leaves. If the light falls on a shoot more intensely on one side than another, the rate of growth very speedily changes so as to cause the growing region of the stem to bend or curve till its apex is directed towards the point from which the strongest light is coming.[1] The plant exhibits a power

[1] A figure illustrating this is given in the *Biology* primer, p. 71.

of perceiving or appreciating differences of intensity of illumination. This sensitiveness is of the greatest value to the shoot, for as the stem bends towards the source of the light the leaves which are expanded nearly at right angles to it are exposed to the rays which they need for the manufacture of sugar.

The leaves also manifest an independent sensitiveness to light. They are generally so expanded as to expose their upper surfaces to the sunshine. If this position cannot be attained without a movement of the leaf this movement is effected and supplements the other. The leaf-blade twists on its petiole, or the petiole twists in such a way as to expose the surface of the blade.

With the same sensitiveness to light we see thus that the different members of the plant respond differently, but always purposefully, to it. The root grows away from the incident rays, penetrating into the deeper crevices of the soil; the stem grows towards them, while the leaf places itself across their path.

The positions assumed by the stem, branches, and leaves are greatly influenced by the various stimulations they receive; some respond more actively to one, others to another; but all show both perception and response as they adapt themselves to their environment.

CHAPTER VII

THE STRUCTURE OF THE SHOOT

WE must now examine what are the arrangements of the internal structures of the shoot which enable it to carry on these duties. Though the shoot is to be regarded as a single system comparable with the root, the duties discharged by its cylindrical and its flattened parts are so far distinct that it will be well to consider them separately from our present point of view.

When we examine the plumule we find it to be composed of cells resembling those of the radicle. They are at first all alike, and only slowly do differences become apparent. At the apex we find them meristematic, that is, each cell has the power to divide into two. A little farther back they increase in size and become vacuolated. If we take a longitudinal section at this age, we find that, as in the root, we can distinguish three regions which are faintly indicated (Fig. 24). The central strand or plerome is visible, appearing conical in shape as in the root. Outside it lies a periblem, and this is covered by a dermatogen, a layer of a single cell in thickness. These two are not conical, but are thrown into irregularity by the outgrowth of the leaves. The leaves and branches differ in their origin from the branches of the root as they begin with the outgrowth of the periblem, which pushes the dermatogen before it. The plerome takes no part in their formation. As the plumule gets older its elongation proceeds by the continued formation of new cells and their subsequent growth. This goes on for some time, and extends as a rule further back than it does in the root. The growing region is a little more complex in the stem than in the root, because the cells do not all grow alike, those of the nodes, or places where the leaves arise, elongating scarcely at all, while

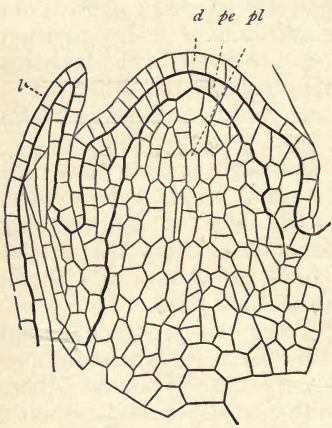

FIG. 24. Growing point of stem of Dicotyledon. *d*, dermatogen; *pe*, periblem; *pl*, plerome; *l*, young leaf. (After Scott.)

those of the internodes are very vigorous. The leaves on the nodes elongate from the first, but the branches in their axils appear much later.

As the seedling grows, it prepares for the discharge of the duties which devolve upon it. What we are about to describe of its structure corresponds almost exactly with the structure of each year's twigs of the tree or shrub into which ultimately it develops.

The two main duties of the stem we have seen to be the support of the head or leaf-bearing part of the shoot and the transport of the water and mineral compounds absorbed by the roots to the seat of construction of organic substance. Both these objects are carried out by the arrangements in the central cylinder, and both depend upon the development of vascular strands connected with those of the root. If we look at a longitudinal section of a whole plant we find that these strands are continuous throughout it though they are arranged differently in its different regions. In the root we found the strands of wood lying sometimes separately in a central ring, sometimes joined to form a solid cone of wood. Other strands, soft in nature, known as *bast*, lie between them or between their outer limbs when they are fused in the centre. As we pass upwards we find that in the region just below the cotyledons a certain rearrangement of the strands takes place. The bundles shift their relative positions and the wood strands come

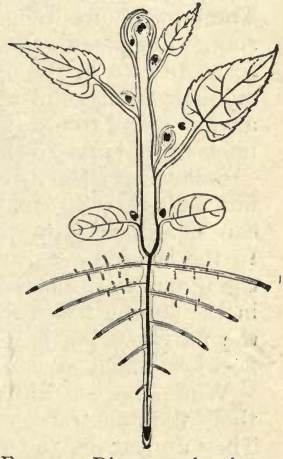

FIG. 25. Diagram showing the general structure of a dicotyledonous plant.

to lie exactly inside the bast strands, the two being separated only by a layer of meristematic cells known as *cambium*. The bundles in the shoot are known as *conjoint* bundles from this association of the wood and bast. The wood strands, further, become twisted on their long axes in this same region, so that the protoxylem, which in the root is on the outside, is in the stem on the inner face. The bundles are wedge-shaped much as they are in the root. Each seems thus to have turned completely round so as to face in the opposite direction. Instead of the cylinder being solid in the centre, the conjoint strands always stand round its periphery so that there is a large unoccupied space in the centre, known as the *pith*.

Following them to the growing end of the stem we find that they do not terminate in its growing cells, but can be traced into the leaves through their petioles. In the latter they usually form a half cylinder open on the upper side, instead of a complete hollow cylinder as in the stem. From the petiole they can be traced into the flattened portion of the leaf, where they form the network which we call the *veins* of the leaf.

While the leaf and stem are very young we find in them the first traces of the origination of these strands. They appear in the growing point a little way back, as separate strands in the plerome, made up of small cells, longer than broad, defined from the rest chiefly by their smaller transverse diameters. They are all meristematic and only slowly lose the power of dividing. A transverse section (Fig. 26) of the plerome shows these little strands as wedge-shaped areas, the procambial strands, arranged in a circle near the outside of the plerome, separated by narrow areas known as *medullary rays*. As they get older the cells become changed into their adult form. The change in the wood cells is associated with growth in diameter and irregular thickening of the walls, making them appear as if marked out into

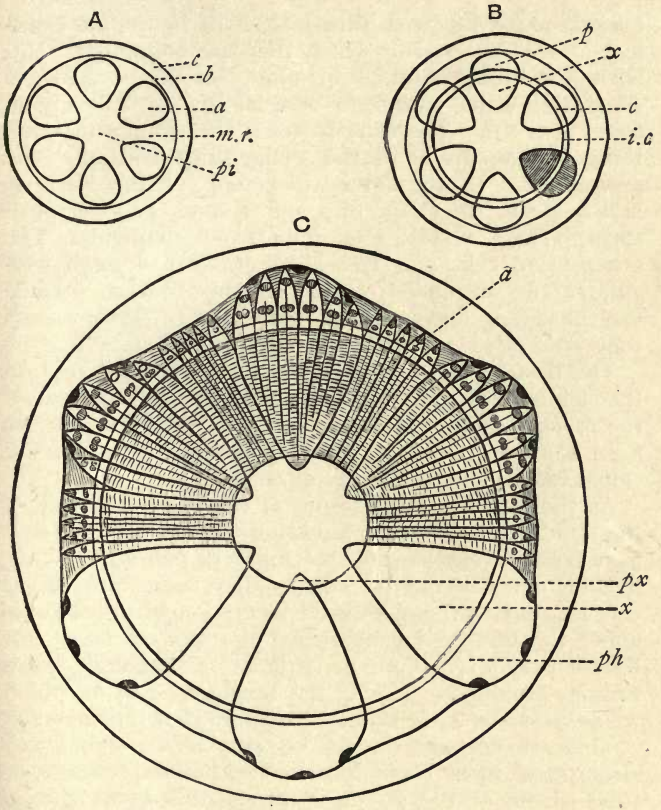

FIG. 26. Diagram of sections of stem of dicotyledon at three ages. A, young condition, showing commencement of differentiation of the plerome and its vascular strands: *a*, strand; *b*, limits of the plerome; *c*, periblem; *m.r.*, medullary ray; *pi*, pith. B, a little older stage: *p*, bast; *x*, wood; *c*, cambium; *i.c.*, interfascicular cambium: (one of the strands has been shaded). C, older stage, after the commencement of secondary thickening: *px*, protoxylem or first-formed wood; *x*, secondary wood; *ph*, secondary bast. (After Sachs.)

curious patterns; with substitution of lignin for cellulose as the material of which they are composed; and with the disappearance of many of the transverse separating walls, causing a vertical row of cells to become a vessel. The cells to show the change first are those on the inside of the wedge-shaped strand—the *protoxylem.* In these the thickening of the walls is laid down in the shape of a spiral band, or a series of rings. These vessels remain of small diameter. The other wood cells and vessels are thickened more irregularly and are called *reticulated;* in some cases when the thickening deposit leaves only very small thin spots they are known as *pitted* elements (Fig. 13, p. 35).

The bast of the strand begins to be differentiated on the side nearest the periphery, where the cells are called the *protophloëm.* The vessels of the bast are sieve tubes (Fig. 27) as in the root. The other elements are mainly elongated cells with thin cellulose walls.

As the differentiation begins at the front and back of the bundle and advances in each direction the wood and bast are not very long in meeting. In plants that only live for a few weeks or months they come into actual contact, but to those whose lives are longer provision is made for further development by the last layer left between them remaining meristematic or capable of continuous dividing. This is the *cambium layer* of which we have spoken. It is only a single cell in thickness.

This arrangement of the supporting tissue is very strong and most economical. The hollow cylinder or tube is one of the strongest forms of support that a structure can possess. It has, too, a certain flexibility, for while the strands are gradually hardening they can bend freely without breaking. The young stem thus shows itself built for toughness and elasticity, so possessing a power of bending to wind and recovering as the force of the air passes it. The continuity of the

vascular strands throughout the plant ensures the proper distribution of the water absorbed from the soil.

Certain other features of the framework of the plant next call for attention. If we examine the outer layer, called in the stem and leaf the *epidermis*, we find it as a continuous sheet over the whole, and in most cases a

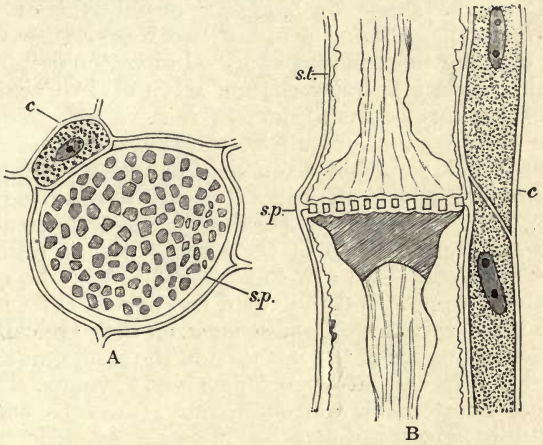

FIG. 27. Sieve tube from stem of *Cucurbita*. A, transverse; B, longitudinal section; *s.p.*, sieve plate; *c*, companion cell. (After Strasburger.) ×500.

single cell in thickness. A delicate structure like a seedling, whose cells are filled with water, is exposed to a general evaporation at the surface. This, if not guarded against, would lead to a loss of water beyond the control of the plant, and would interfere with the proper conduction of the water to the places where the construction of sugar takes place. We find a very simple but very effective protective mechanism. The outer walls of the cells of the epidermis become thickened and their external layers are changed into a very impermeable

material called *cutin*. These external layers can be stripped off from large pieces of the surface in a kind of pellicle, which is known as the *cuticle*. It is developed more freely over the leaves than over the stem.

This layer serves too as a protection against cold. For this purpose many plants have an additional safeguard, in the shape of hairs, or outgrowths of the epidermal cells, forming a fine feltwork over their surfaces, clothing them indeed in a kind of cotton garment.

Both cuticle and hairy coating serve also to protect the delicate surface from injury by rain.

The outer coating or cuticle, covering as it does the whole exterior, would be a source of danger to the plant by preventing almost all evaporation, if it were altogether intact. The epidermis is pierced by small apertures, which are the openings of the system of intercellular spaces or passages we saw to be developed in the root and which we now find to extend throughout the whole of the shoot as well. These *stomata*, as they are called, are more numerous in the leaf than in the stem, but they are present in the latter so long as it is young. The aperture or stoma is surrounded by two cells called guard-cells, which are attached together at their ends but not in their centre. They are kidney-shaped in appearance, and when filled with water they stretch so as to draw apart in the centre, opening the stoma (Fig. 28). When the water is withdrawn from them they fall together and close the aperture. This arrangement thus allows the necessary evaporation of water to take place. The vapour is formed in the intercellular passages and passes out through the stomata, the width of the apertures being regulated by the amount of water in the guard-cells, which in turn depends on the amount of water in the plant.

The layer of cells between the central cylinder and the epidermis, which is the continuation backwards of

the periblem, is the *cortex*. Its composition is very varied as the plants grow older. In the young condition it is only noteworthy because its outer layers of cells contain the green bodies we have called *chloroplasts*.

The great development of branching which takes

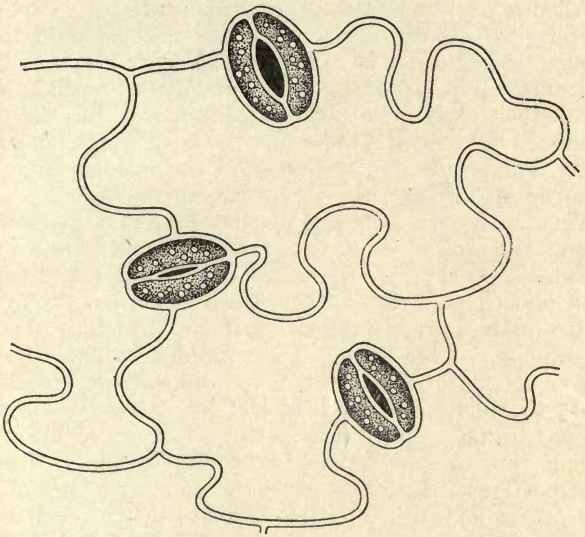

FIG. 28. Epidermal cells of leaf showing three stomata in various stages of opening.

place necessitates a considerable enlargement of this primary structure. The increase in number of the leaves makes it important to increase the means of transport of water; the slender cylindrical tube of the young stem soon becomes unable to support the weight resulting from its greater size and the number of its branches. The transport of food to its different parts makes increasing demands upon its bast. We must examine the way in which these necessities are supplied.

As the stem grows we find additional vascular strands continually being developed, a change directed especially to the strengthening of the stem, as the new strands are not directly connected with the leaves. The original strands also are much enlarged and strengthened.

All this work is done by the cambium layer. Part of the original bundles, as we have seen, consists of this tissue, which is hence called *fascicular* cambium. By continual division of its cells, mainly in a direction parallel with the outside of the stem, masses of cells are produced between the wood and the bast. One layer of these remains cambium—those on the inside of it are changed into wood, those on its outside into bast.

Very soon after this process has been set up in the bundle the cells which lie between the strands, known as the *medullary rays*, are the seat of change. No doubt the multiplication of the cells of the cambium sets up a strain in the ray cells adjoining them, stretching them, or dragging upon them. The stimulus of this strain makes certain of these cells, extending across the ray, begin to divide in their turn, and soon the rays are all crossed by layers of meristematic cells, joining up into a ring the isolated cambiums of the bundles. These new portions, which complete the ring, are known as *interfascicular* cambium. The whole ring now behaves as the original cambium of the bundles does, and soon a ring of wood is formed in front of and a ring of bast behind it. The parts of the ring formed by the interfascicular cambium have no connection directly with the leaves.

As new leaves arise at the apices of the twigs the vascular strands belonging to them are connected with this vascular cylinder as were the primary ones, for the structure of the young twigs resembles in all points that which we have described for the seedling.

At the end of each year, in our climate, the growth of most trees ceases, owing to the fact that the leaves fall

off. When it is resumed on the putting out of the leaves of the next year this process recommences. There is a difference in appearance between the wood

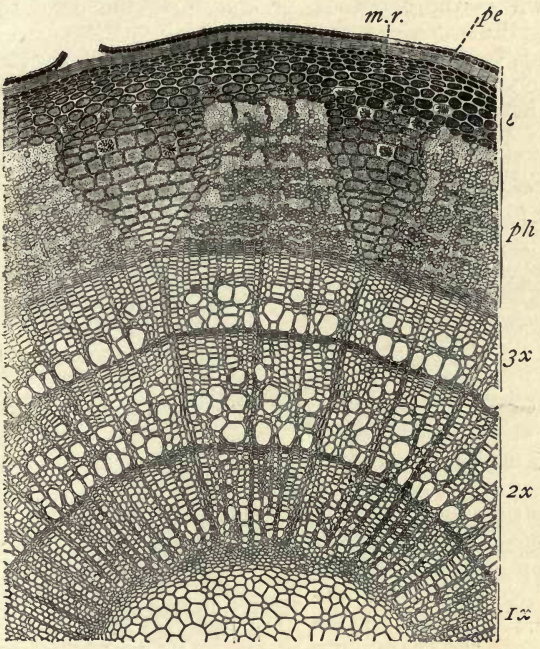

FIG. 29. Section of twig of lime-tree, 3 years old. 1*x*, 2*x*, 3*x*, the successive annual rings of wood. (After Kny.)

formed at the end of the season and at the beginning, so that the formation of each year stands out distinct from that of the next, when a transverse section of a twig or branch is examined. Each year's formation is spoken of as an *annual ring*. The rings of wood are easily seen, but those of bast are not so conspicuous (Fig. 29).

When a tree gets old the central part of its wood usually dies and becomes very hard. The only living wood is a narrow area close to the cambium. This is known as the *sap-wood*, or *alburnum*, the dead centre being the *heartwood* or *duramen*.

This substitution of a solid core for a hollow cylinder of wood is necessary for the strengthening of the trunk and branches. In this well-developed form the mass of the body of both shoot and root is made up of hard wood.

As the trunk and branches gradually thicken, their outer regions are strengthened by the production of *bark*. This begins in the stem as in the root by the formation of sheets of cork. In the root these layers arise in the pericycle; in the stem they begin in the cortex just below the epidermis (Fig. 30). As the years pass, more and more layers of cork are formed deeper and deeper in this region. The outer ones are pierced by lenticels (Fig. 31). They are all formed in the same way, by the formation of meristematic layers, which produce cork in their outside and add to the cortex on their inner faces, behaving in much the same way as the cambium, though the cells they form do not give rise to bast and wood. The cork is impermeable to water and consequently all the cells outside the innermost layer of it die; the tissue thus formed constitutes the bark (Fig. 32). As the years go on it becomes thicker and thicker and much

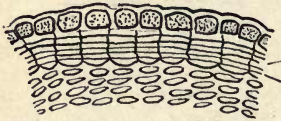

FIG. 30. Commencement of cork formation in stem.

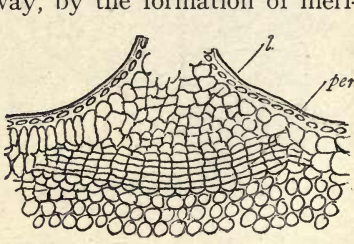

FIG. 31. Section of a lenticel, *l*; *per.*, cork layer.

crinkled and split up through the action of the weather and the storms the tree is exposed to.

We must now examine the interior arrangements of the leaf. We have already learnt that its special work is mainly twofold. It is the chief agent in transpira-

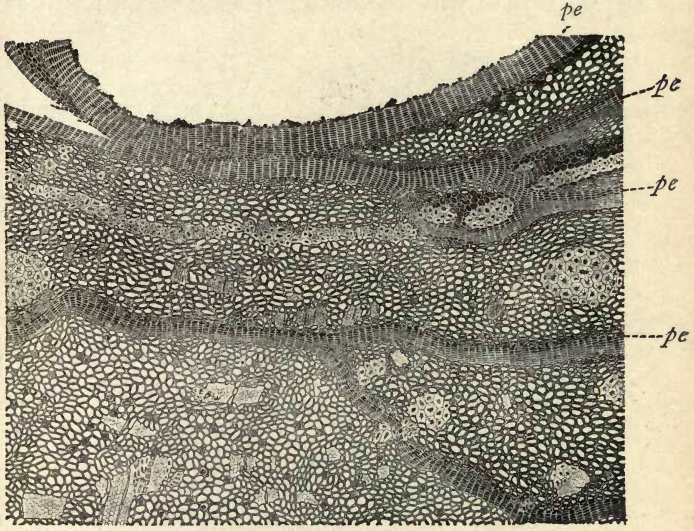

FIG. 32. Section of bark of *Quercus*. *pe*, cork layers arising at different depths in the cortex. (After Kny.)

tion or the evaporation of the water which the plant does not permanently retain; while it also is the chief seat of the construction of organic food substance. These two duties are discharged mainly by the cells of the lower and of the upper halves of the leaf respectively.

The petiole or stalk of the leaf has a general structure not unlike that of the stem, except that its vascular strands do not form a complete cylinder, but only half

a one, being open on the upper side (Fig. 33). The petiole is generally not cylindrical in shape, but flattened on the upper face. It is continued with little change of structure into the blade, where it appears as the mid-rib.

The blade of a stalked leaf is the ultimate portion of the outgrowth with the flattened wing which has been

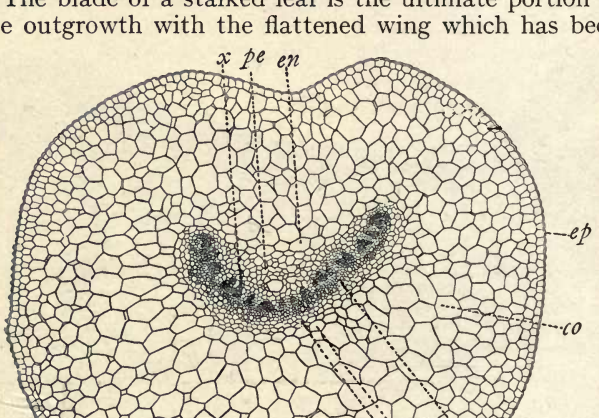

FIG. 33. Section of petiole of *Primula sinensis*. *ep*, epidermis; *co*, cortex; *en*, endodermis; *pe*, pericycle; *ph*, bast; *x*, wood.

developed along its two edges. The part between the two wings is generally known as the mid-rib. If we cut a section through the blade (Fig. 20) we find its structure adapted to the work for which the flat part was developed. On both surfaces we find an epidermis, the lower one especially pierced with stomata. Under the upper epidermis the cells are long and narrow and arranged side by side much like the vertical railings of a fence. They touch each other along nearly their

whole length, intercellular spaces being small and not numerous. There may be only one layer or several layers of these cells, which constitute what is known as the *palissade* tissue. The cells contain numerous chloroplasts, which are embedded in their protoplasm. Each has as usual a central vacuole filled with water. These chloroplasts are capable of a little movement in the cell. It is in this layer, exposed to the light most freely, that the sugar is constructed. (*See* Fig. 20, p. 52.)

The lower half of the leaf is made of cells which are spherical, cubical, or oblong, and are arranged so as to touch each other only at few points; consequently the intercellular passages between them are very large, taking up sometimes more space than the actual cells. This is often called the *spongy* tissue of the leaf. The cells contain some chloroplasts, but not nearly so many as the palissade cells. This layer is the layer in which evaporation occurs. The veins generally run in the centre of the blade, between these two layers of cells.

All the structures of both petiole and blade thus show exact adaptation to the two main duties of the leaf.

CHAPTER VIII

THE MONOCOTYLEDONOUS PLANT

Our attention has been mainly directed so far to the peculiarities of the dicotyledonous plant. We must now turn for a little while to study another form, in which the embryo has only one cotyledon. The plants of this type are not so numerous as the former class, but they are still very widespread. The most easily accessible of them in this country are the grasses and the group which is represented by the common white lily.

If we take a grain of wheat we have what is very generally spoken of as the seed of the plant. This is

not strictly accurate; it is really the fruit and contains the seed, but the testa of the seed and the wall of the fruit are so closely united that we cannot separate them. The grain of wheat is a small ovoid body with one side flattened and grooved down its length. At the back, quite at the lower end of the grain, is a little wrinkled area, which marks the position of the embryo, above which and forming the greater part of the grain is the endosperm, filled with food for the young plant during its early growth or germination. A section of the grain is shown in Fig. 34.

FIG. 34. Longitudinal section of grain of oat.

The grass embryo possesses a single large cotyledon which is at first terminal and continuous in a straight line with the radicle, while the plumule grows out laterally some little distance below the apex. As it grows the cotyledon becomes forced over to one side, and the plumule and radicle come to lie in a straight line, as in the dicotyledons. The cotyledon then develops along the side of the rest of the embryo, separating it from the endosperm. The side of it which is in contact with the latter is the part which absorbs the food in the endosperm cells. In other seeds the cotyledon remains in a line with the radicle, the whole embryo being surrounded by the endosperm. In germination, however, the upper end of the cotyledon is the last to leave the seed coat, remaining there and absorbing the endosperm as long as any persists.

If we soak some grains of wheat or barley and keep them warm germination soon begins. The radicle protrudes as a little white body from the micropyle; looking along the back of the grain we can notice a little pointed prominence gradually making its way in the other direction under the skin and ultimately emerging at the other end; this is the plumule. As it gets larger it dis-

places the rest of the grain, which comes to lie on the side of the young plantlet. The grain remains underground.

The further development is different from that of the dicotyledon. The root does not form a tap root, but branches almost at once; indeed in the grasses generally it begins to do so before it escapes from the grain. The main root grows scarcely at all, but a number of branches arise behind its apex, making in the grasses a cluster of delicate fibrous rootlets. The growth of the young stem is seen more advantageously in a larger grass —the maize. At first it is very slender, but as development proceeds its growing point becomes continually larger and more vigorous, so that each node and internode become larger than the preceding ones. The young stem has thus the form of an inverted cone (Fig. 35). This goes on till the plant reaches a certain height, when this continuous enlargement ceases and the later parts of the stem are cylindrical. Several roots are developed from the nodes of the lower part of the stem in the case of most monocotyledons; as they arise out of the normal order they are called *adventitious* roots.

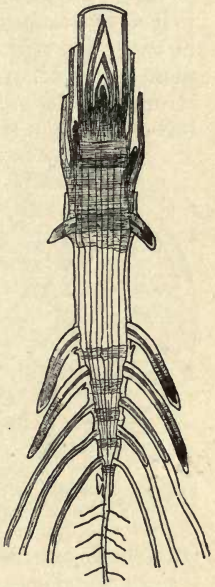

FIG. 35. Diagram of mode of growth of stem of monocotyledon (*Zea*). (After Sachs.)

The stem of the monocotyledon produces as a rule one leaf at each node. This leaf has a very broad base, which encircles the stem in large part, or sometimes entirely. The leaves are said to be *sheathing*.

The general requirements of the plant are not very different from those of the dicotyledon and need not

therefore be discussed at any length. The distribution of the conducting tissues is, however, materially different so far as the stem is concerned. The root has its strands placed like those of the dicotyledon, but it never increases in thickness and does not show, therefore, any development of cambium or secondary woody elements. The strands in the stem are confined to the central cylinder, but each conjoint strand of bast and wood passes up the stem separately. Each is surrounded by a protecting sheath of hardened cells and never contains any cambium. The strands are numerous and are arranged in a series of circles. When the number is very great this circular arrangement cannot easily be seen and the strands appear to be scattered thickly through the central cylinder (Fig. 36). They are found to be continuous with similar strands in the leaf, which as before are called the veins. These run in the main parallel to one another, and do not form the complex network which is seen in the leaf of a dicotyledon.

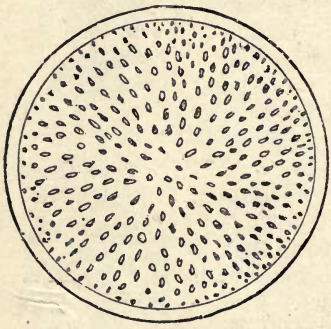

FIG. 36. Diagram of transverse section of stem of monocotyledon.

The relations of the leaf to the stem are a little different from those of most dicotyledons. The bases of the leaves sheathe the stem and do not as a rule fall off in autumn. The leaf, however, sooner or later dies, but its base remains where it was. As the stem grows older, as in the case of many palms, these leaf bases cover nearly the whole of the trunk, causing the latter to appear much thicker than it really is.

The leaf has palissade parenchyma in a narrow layer under both surfaces.

CHAPTER IX

THE FOOD OF PLANTS

We have in our introductory chapter considered in outline the important question of the nutrition of plants, a subject which has been treated of also in Chapter VI. of the primer of *Biology*. It is necessary now to return to this subject and examine it a little more fully.

The substances that are taken in by a plant are the carbon dioxide which is present in the air, and the water and dissolved mineral matters which the roots obtain from the soil. We must again emphasise the fact that these materials are not capable of serving as food in the condition in which they are absorbed, but that a great deal of work has to be carried out to convert them into nutritive material. It is only the green plant which can build them up into such compounds as the living substance can incorporate into itself, the work being effected by the chloroplasts, the little ovoid bodies which are the seat of the green colouring matter. Further, the chloroplasts can only work when they are properly illuminated.

The carbon dioxide exists in very small proportion in the air, not more than about 3 parts being present in 10,000. The gas enters the plant by way of the stomata, and so makes its way into the intercellular spaces whence it obtains access to the cells in which the chloroplasts are present. The water from the soil is conducted in the way we have described to the same cells, continually replenishing the supply in their vacuoles. We have thus present in the cells of the parenchyma of the leaf a supply of carbon dioxide, water, and the chloroplasts themselves. When sunlight shines upon the leaves in appropriate intensity the constructive action commences. The stages are not yet fully understood, but there appears to be no doubt that in some way the chloroplasts cause a certain chemical action to be set

up; the carbon dioxide and some of the water disappear and are replaced by a simple organic substance known as formaldehyde, while a quantity of oxygen, equal in volume to the carbon dioxide, is set free. The oxygen finds its way from the cells into the intercellular spaces and passes out of the plant by way of the stomata. Formaldehyde is thus the first organic product which is formed; it is a gaseous body and probably is never present in any but very small quantities, for it is almost immediately transformed into a kind of sugar. The manufacture of sugar is thus the first stage in the preparation of the food of the plant.

This construction of sugar cannot be carried out without the application of energy. We are familiar, from our ordinary experience of things, with the fact that a machine cannot be made to do work without a supply of energy. A steam engine cannot work without the expenditure of a certain amount of fuel. Whence then does the chloroplast obtain the energy which it applies to sugar-making? The answer to this question explains the necessity for the proper illumination which we have spoken of as a condition of its activity. The rays from the sun, which we speak of as the rays of light, are absorbed by the green colouring matter of the chloroplast. We can prove this by the use of an instrument known as the spectroscope, which is an arrangement of glass prisms. If we let a beam of white light from the sun fall upon such a prism the rays of which it is composed are bent or deflected unequally on entering and leaving the glass, so that if they are allowed on emerging to fall upon a plane surface they appear as a broad band of light showing a series of colours ranging in order from red to orange, yellow, green, blue, and violet. If now we place a thin film of a solution of chlorophyll between the source of light and the prism we find all the rays do not reach the glass, so that the

coloured band which emerges is not continuous, certain parts of it being blotted out. The *spectrum*, as the band is called, is consequently crossed vertically by a number of dark bands, corresponding to the position of the missing rays. In the living cell these rays are absorbed by the chlorophyll exactly as they are by the solution used in the experiment, and it is from them the plant derives the energy which is used. The rays which are most active are a certain number of the red ones; these correspond in position with a broad black band which is one of those described.

This process of sugar construction can only take place at a moderate temperature.

Another very important constituent of the plant's food is *protein*, which differs from the group of foodstuffs to which sugar belongs by containing nitrogen in combination. Very little is at present known of the processes by which protein is made. Compounds of nitrogen, preferably nitrates of potassium, calcium, magnesium, or ammonia, are absorbed by the roots, dissolved in the water which they take in. The changes they undergo lead in some still unexplained manner to the formation of much more complex nitrogen compounds, which are generally though not strictly accurately described as *amides*. Among them may be mentioned asparagin, leucin, and tyrosin.

By still further changes these are converted into proteins, but the chemistry of the process is still obscure.

A third constituent of the food of plants is fat or oil. This is less widely distributed and appears for the most part only in places of storage. It is formed directly from the living substance there and does not appear to be built up from simple substances in the plant.

Sugar is a member of a group of substances which are called *carbohydrates*. It is formed in large quantities when the chloroplasts are properly illuminated; much

more is made than is needed for immediate use. The surplus is immediately deposited in the chloroplasts in the form of grains of *starch*. Starch is another carbohydrate which very readily becomes transformed into sugar by the action of dilute mineral acids or of a peculiar body known as *diastase*, which is a digestive ferment or enzyme. Probably an excess of protein is also made while the conditions are favourable.

The cells in which these foodstuffs are made have to manufacture sufficient food not for themselves only, but for the whole plant, many of whose cells, as we have seen, are set apart for other purposes altogether. It is necessary accordingly for the food to be made in large quantities and for the surplus to be transported from the cells in which it is made to the other cells of the organism. Part of it is devoted to the nutrition and growth of the body of the plant, and a large amount is stored in various places to nourish the reproductive organs.

There is consequently a continuous movement of the manufactured food substances about the plant. The sugar temporarily deposited as starch grains in the chloroplasts is taken away as soon as darkness falls. The ferment or enzyme *diastase*, which is present in the cells, converts the starch into another form of sugar, which diffuses outwards. A stream of such sugar is thus leaving the leaf during the night and passing to other cells of the plant, either to be consumed in the growth processes or to be stored up till wanted. Probably this stream of sugar is passing also during the day, but while the manufacture is going on it is not easy to detect it.

When proteins leave the cell they are first converted by a similar ferment into the amides we have spoken of and pass through the plant's tissues as such.

Sugar and either proteins or amides are taken up by the living protoplasm and incorporated into its substance. This is the true assimilation, or nutrition of the plant.

The foodstuffs that are stored instead of being directly consumed, undergo a transformation which is the opposite of that to which the enzymes give rise. The sugar is converted again into starch, a process carried out by certain plastids much like chloroplasts, but without any green pigment. These *leucoplasts*, as they are called, are present in the cells in which the storage takes place. The amides are built up again into proteins and deposited in the cells. In seeds they appear as peculiar grains of protein matter, which have long been known under the name of *aleurone grains*. They are formed by the protoplasm of the cell and not by any plastid.

The transport of these streams of food material is effected chiefly by those soft parts of the vascular strands of which we have spoken as bast or phloëm.

CHAPTER X

THE RESPIRATION OF PLANTS

It is a matter of common experience with us all that a certain process called breathing must take place. We know that we are continually taking air into our bodies and passing it out again. What we are not perhaps aware of is that the air we give out differs in two important particulars from that which we take in—it has gained some carbon dioxide and it has lost some oxygen.

What is true of ourselves is true also of plants. During the whole time of their lives they are absorbing oxygen and giving out carbon dioxide, two processes which constitute the beginning and the end of another very complex internal one which is known as *respiration*. So long as active life lasts this interchange of gases can be detected by appropriate methods, though it is observed with difficulty during the daytime on account of the absorption of carbon dioxide and liberation of

oxygen, which we have seen to be associated with the manufacture of sugar. It can, however, be detected by experiments. To prove the absorption of oxygen, take a flask and fit it with an india-rubber stopper through which a glass tube bent twice at right angles can be passed; let the end of the tube dip into mercury in a small vessel standing side by side with the flask. Fill the flask with healthy leaves. In addition to the leaves place in the flask a test tube containing a solution of caustic potash and cork it up so that the outlet tube dips into the mercury. Keep it at a constant temperature for some hours. The mercury will rise gradually into the tube, and will continue to do so for some time, so showing that a diminution of the volume of the air in the flask has taken place. Analysis of the air then left in the flask will show that the volume of nitrogen is unchanged, while that of oxygen has diminished. Examination of the caustic potash will show that it has absorbed an amount of carbon dioxide.

The reason for employing the potash is that the carbon dioxide which is exhaled in respiration is about equal in volume to the oxygen absorbed, so that unless it is removed the diminution of the volume of the oxygen will be compensated for by the addition of the carbon dioxide and the mercury will not rise in the tube.

We can show the exhalation of carbon dioxide by the living plant by means of another experiment. Place a number of leaves in a flask through the stopper of which air can be made to enter by one glass tube and can be removed by another. Make the air as it enters pass through a bottle containing a solution of caustic potash which will free it from all traces of carbon dioxide. Pump the air through the flask by means of some form of air pump or aspirator and lead it through a bottle of lime-water. It will soon make the lime-water milky in consequence of the formation of carbonate of calcium,

brought about by the reaction of carbon dioxide with the lime. As all carbon dioxide was kept from entering the flask, and as the lime-water shows by becoming milky that some of this gas reached it in the stream of air pumped through it, it becomes perfectly clear that the plant has exhaled it.[1]

Besides carbon dioxide a certain amount of water vapour is exhaled by the plant in the process of respiration.

To understand the purpose of respiration we must go back a little and consider some of the features of sugar manufacture. We saw that the energy for this work is derived from the sun. The work it does is to build up sugar and subsequently other compounds, which remain in the plant. These substances retain in themselves the energy which was expended in making them. When they are decomposed or reduced to simple compounds like those from which they were made, this energy can be liberated again. If we burn them, for instance, we get the liberation of a large amount of heat, which can be made to do work in other directions. So we see that the construction of the plant, both living and non-living substance, involves the fixation of large amounts of energy as well as of material.

The purpose of respiration, which involves the breaking down of the living substance incidental to its wear and tear and the work it does, is in this way to liberate the energy without which these operations could not take place.

CHAPTER XI

THE EVOLUTION OF THE FORMS OF PLANTS—ALGÆ

THE considerations set out in the foregoing chapters apply in great part only to the higher terrestrial plants. But the whole range of vegetation is much more exten-

[1] A form of the apparatus is shown in the primer of *Biology*, p. 56.

sive than this. There are many other types of plants which differ from the land plant we have considered and differ too among themselves in many respects. They live in various situations, they attain to very different dimensions, and they show a great variety in the details of their internal structure. A very large number of plants, some very humble, others very elaborate, in degree of development, live altogether or almost entirely in water. Many others of simple structure occupy moist situations, such as rocks on the banks of streams, damp earth, or trunks of trees near the ground; others again dwell in hot, arid regions where little water can reach them. Nearly all these forms resemble the higher plants in possessing the green colouring matter; but there are others which have lost it, and which live, therefore, on decaying matter or in the bodies of other plants or of animals.

If we consider the whole mass of vegetation and compare the simple forms we find with others of much complexity, we come to see that there is and has been throughout it a continual advance, though a very slow one, in the direction of greater complexity. This leads us to believe that the most highly organised plants we see to-day have been developed from extremely simple ones during the long ages of the past.

If we try to determine how this has taken place we are able to form some idea of its course by studying the simple plants existing at the present time and the gradual increase in complexity we can find among them. Very probably the different forms show us the different stages through which development has passed.

The simplest plant we find to-day is a very small structure living in water. It consists of a single piece of protoplasm with its nucleus; it is clothed by a thin cell wall and contains the green colouring matter. We can suppose without much fear of mistake that the first

plant that existed was not very different from this, and like it dwelt in water. Nor are we likely to be wrong in thinking that the whole group of the seaweeds arose by gradual development from such a form, perhaps before any plants grew upon the surface of the land. If we examine this group of seaweeds we find a succession of forms which are step by step more elaborate, and we see therein some justification for thinking that development or evolution has proceeded on similar lines. There are two points that may well be insisted upon as a preliminary to thinking about these changes: first, there is a predisposition in the living substance to become more highly organised; second, this organisation is brought about by the action, direct or indirect, of the surroundings, the plant succeeding best which is in the most complete harmony with them. We have already illustrated the second of these points so far as the higher land plant is concerned.

It is possible that the original ancestors of the seaweeds were even simpler than the one we have described, not possessing any cell wall. If so, the exposure of the living substance to the changes in the water and to contact with obstacles in it no doubt led to the formation of this cell wall for purposes of protection.

The development of this membrane round it, however, introduced a difficulty in its relations with the water, free access to which for so many reasons was very necessary to its welfare. We can understand that the development of the vacuole, with its little store of water, was speedily effected to obviate this difficulty.

Increase of size of the protoplast was no doubt one of the early features of the life of the plant. This in the condition of a cell clothed by a membrane was only possible up to a certain point without weakening the membrane and so disturbing the protection it had secured. Growth was consequently followed by divi-

sion into two and the gradual separation of the two from one another. Here we see the simplest form of reproduction following growth, each of the two protoplasts resulting from the division possessing the same properties as the original cell. When in some cases the processes of growth and division became very rapid, a second division might well take place in the two new cells before they had become separated. There would arise in this way by degrees a new form of plant, one in which the processes of division continued, but the cells did not separate at all, so that a chain or filament of cells resulted. They would keep their individuality at first at any rate, being almost as independent of each other as if they had separated, their attachment being mainly mechanical. We find a very large number of water-weeds, or algæ, existing in our ponds and streams to-day which have just this structure.

The maintenance of this thread-like structure depends on the cells always dividing in such a way that the new cell walls arise across the length of the thread. It seems certain that this course was soon departed from by some of the plants and that some divisions arose at right angles to the others. This led to the formation of a flat plate of cells, still only one cell thick. A plant with this structure would meet with very little greater difficulty than the thread-like forms; the requirements of the cells would be the same, though the plant might easily grow very much larger, the number of its protoplasts or cells often amounting to many hundreds. Still the cells would be all alike and probably all independent, for water would have access to each and no further provision would be called for. Plants of this type of structure are still common among marine seaweeds.

A great complexity, however, would arise if the protoplasts began to divide in three planes, each at right angles to the other two. No doubt this was not

long delayed, and plants began to possess a bulk or mass, instead of being filaments or one-layered plates. This was a most important change, for it altered the relations between the cells or protoplasts of the plant and the surrounding water. Only the external cells in such a mass were able to absorb water and the inner ones had to depend on them for a supply. The external cells, too, were those which ran the greatest risks from changes of temperature in the water and from contact with particles in it, or the many dangers which the environment brings to the plant. These dangers and difficulties must have increased as the plant itself grew larger. The difficulties of the internal cells were different, but no less serious. They were compelled to draw upon the external ones for the renewal of the water in their vacuoles, for the oxygen necessary for breathing, for their food or its constituents, and for the removal of any waste products they might produce. So the two became gradually less and less like each other, or more *specialised*. The gradual change of structure and form of plants that followed can be traced in this way to the need for adapting them to their conditions of life.

We can follow with some probability the further course of events. As the bulk increased the external cells became still more devoted to protection and absorption; the internal ones ceased to develop chlorophyll as less light reached them, and the work of food construction which is the function of the chlorophyll was thus thrown upon the outer layers. Among the internal mass certain cells became concerned mainly in conducting the water to the rest, so supplying them with oxygen and food. As the size became still greater the exterior surface of the still symmetrical spheroidal or spherical plant became inadequate to supply all that the inner mass required; the spherical plant no longer had sufficient surface in proportion to its bulk. This involved

the restriction of growth mainly to certain regions of the surface, which became what we now call *growing points;* here the multiplication of cells led to the formation of conical outgrowths, and these in turn were soon recognisable as branches. The larger the plant became the more necessary was it for it to become branched in view of the dangers from storms, and currents in the water, as it would oppose much less resistance to the movements of the stream or tide.

The problem of the passage of the absorbed water, as it made its way from exterior to interior cells, involved the question of its being able to pass through the cell walls that lay in its way. As the length of the body of the plant increased with the putting out of branches, the number of the cell walls became an inconvenient obstacle to its passage. The flow being in a particular direction caused the cells to stretch a little accordingly and so to make them become a little longer than broad. This elongation soon became advantageous, as with cells of that shape there were fewer walls to pass in a given distance. So gradually in the regions of transport elongated cells became most usual. After a time the end walls became perforated and later still dissolved altogether, so that the water could pass easily along a tract which was originally a number of columns of cells. We can observe this change of internal structure taking place in many plants to-day. Each column when it has lost its end walls forms a vessel. We find them fully developed only in terrestrial plants, but some of the larger seaweeds contain structures much like them, the end walls being perforated very freely.

During the time these changes were taking place in the arrangements of the interior, other signs of specialisation of exterior parts made themselves visible. With increase of size and great flexibility of body as in the filamentous forms it became advantageous to be

attached to some substratum and no longer passively floated about. So attaching organs were developed; in some of the simple filaments they were only a modified cell at the basal end of the thread; in the bulky plants the whole of the unbranched end was often specially modified to form a kind of grasping organ capable of growing round stones or into crevices.

We find such anchorage mechanisms still in the larger seaweeds of our coasts. These organs are not true roots, for they anchor the plant only, and do not absorb nutritive or mineral compounds for its use.

Such a development of the body of the plant was sufficient for aquatic plants such as seaweeds. Even in the largest of them there is only a very slight specialisation of structure compared with that which is necessary for plants when they come to live on land. We can, however, find in many present day forms three systems of tissues, an external protective and absorbing coat, a conducting system, and between them a system of cells belonging to neither, whose function so far has not been very apparent to us. We see that the division of the body of the plant into members does not go so far as to enable us to recognise what we call stem, leaf, or root. It is in some cases undivided, in others very much branched, but its structure is practically the same throughout. We speak of such a form of plant as a *thallus*, whether branched or simple, massive or minute.

CHAPTER XII

THE DEVELOPMENT OF THE REPRODUCTIVE PROCESSES IN THE ALGÆ

While these changes were occurring in the form and structure of the body of the plant, other developments were taking place in the ways in which new individuals

arose. While plants had only a unicellular body, the division of the cell caused the appearance of a new individual. In fact, the individual was the same thing as the cell. But when the cells failed to separate this ceased to be the case, and the individual plant became identified with the chain of cells. Division of a cell so added another link to the chain, but it did not produce a new individual. For a time the simple method of reproduction by cell division was replaced by the breaking of the chain into a number of segments, each of which grew into a new filament like the first. This method of reproduction is shown now by certain blue-green algæ and by many fungi.

These simple methods, however, led to the production of comparatively few offspring. A larger number became desirable if a species was to hold its own in the competition with its neighbours for what the surroundings afforded, particularly as the life of any individual was but short. So there arose in the plant body special cells, usually in great numbers, which could be detached and give rise to new individuals. Various forms of these cells are still met with; some with no membrane, able to swim about by means of little protoplasmic thread-like outgrowths, known as cilia, which by rapid vibrations set up currents in the water; some motionless and well protected by firm cell walls, so as to be able to resist heat or cold, and even some degree of drying up. Such little specialised reproductive cells are now generally called *gonidia*. They are still produced in various ways and usually in very large numbers by many of the seaweeds and another group related to them—the fungi. This showed a great advance in the spread of the species, as each of the large number produced could give rise to a new plant.

But such rapid reproduction tends to weaken the race, and no doubt it told its tale in the ancient times. It

was supplemented by another method which gave rise to a renewal of vigour in the offspring. How the new method was first brought about it is hard to say. It can still be seen to play its part among the free swimming gonidia of the seaweeds. Two of them, instead of developing into two plants, fuse completely together to form a single protoplast, which after a period of rest grows into a single new plant. This union of the two is called *conjugation* and the fused product is a *zygote*.

We have in this process an indication of the way in which sex in plants began to be developed. We cannot speak of either of the two conjugating cells in this stage as male or female, but the further development into well-recognisable sexes can be easily traced. One of the cells of the pair became larger and more sluggish than the other; then a stage was reached in which the larger of the two was not motile at all. By and by, instead of being developed from any cell of the plant they came to be produced in particular cells or groups of cells—organs for their development. The smaller active cells came to be recognised as male, the sluggish ones as female. At first they were equally numerous, but as the females became larger fewer of them were formed in the specialised cells. The number varied indeed inversely as the size. While the males continued to be produced in large numbers the females became ultimately solitary in the organs bearing them. Finally the female never escaped from the organ but was joined there by a male. The act of fusion of the two has come to be spoken of as *fertilisation*. The female cell is now known as an *ovum;* the male cells are called *sperms*. There is an almost infinite variety in the modifications which these lowly plants have shown and show to-day in the ways they develop their gonidia and their ova and sperms. We cannot go more deeply into the matter here.

From the elaborate nature of its mechanism, this

sexual process of reproduction led to the appearance of fewer offspring than the method of gonidia production, but those so formed were much more vigorous and better qualified in every way to carry out their vital processes, and hence this process has become almost universal.

This stage does not, however, mark finality among plants. It involved a good deal of uncertainty as to whether fertilisation would take place, as both the parents of the sperm cells and the ova were unable to move except as they were drifted about in the water. The sperm retained the power of swimming when liberated, but the ovum in the higher types remained enclosed in the oögonium or cell in which it was formed. This uncertainty led to a further development, by which one act of fertilisation was made to produce several young plants instead of one. This was brought about by the zygote—the fertilised female cell—dividing up into a number of cells, which were liberated by the bursting of the zygote wall. These cells in most cases were furnished with cilia and in general appearance and behaviour were hardly if at all distinguishable from the gonidia described before. Such reproductive cells can be seen to-day in the alga Œdogonium. To distinguish them from the gonidia they are spoken of as *spores*. One act of fertilisation results in this way in the production of a number of new individuals.

A little further advance still was made among the algæ, which became, however, much more marked among the plants which established themselves on land. Instead of the fertilised cell dividing at once to produce the spores, it developed into a relatively bulky multicellular structure, which became differentiated so that only part of it gave rise to the spores, while the rest served to protect them and to minister to their nutrition. Such a structure can be seen to-day in many of the red seaweeds, in which it is known as a *sporocarp*.

In the land plants, as we shall see presently, this line of development became much more extended. The zygote gave rise to a much more highly organised sporocarp, in which the cells which formed the spores became more restricted in their numbers and disposition. The further progress of development led to much greater differentiation of the sporocarp, which gave it the power of living independently. The sterile part, or the region which did not directly form spores, became much enlarged and grew to dimensions much exceeding those of the original thallus. Its body became differentiated into root, stem, and leaves, and upon the sub-aerial parts the spores were formed in structures known as sporangia. This structure, known as the *sporophyte*, is now the dominant form of all terrestrial plants. We shall consider this change in the next chapter.

CHAPTER XIII

THE ORIGIN OF TERRESTRIAL PLANTS—EVOLUTION OF MOSSES AND FERNS

We must now consider what has been perhaps the most important step we find in the development of vegetation, the transference of plants from water to land. At first all were aquatic, but in the natural course of events no doubt many were washed on to the moist earth by the side of the water in which they were living. Being adapted only to life in water no doubt most perished, and it was only gradually that some established themselves. A comparison of aquatic with terrestrial forms as we find them to-day shows how complete a change in almost every respect took place. In the water the direction of their growth was comparatively unimportant, and a large number grew in a horizontal position. On land we find this extremely rare; most plants, as we

have seen, grow vertically upwards and downwards, and show very different peculiarities in the parts which take these opposite directions. The transference probably did not take place till the habits of reproduction we have briefly described had been acquired. Most likely the first form which secured a footing in the soil was a flattened thallus, consisting perhaps of only a few cells. Its small size would enable it to touch the moist earth over a large part of its surface and so to be able to absorb the water it required. But with multiplication of cells, and consequent increase of size, this became difficult or impossible. It could only reach the moisture in places and the supply so became insufficient. We find such plants now on the earth, and we see that to secure the water supply they have developed outgrowths of their surface cells which resemble root hairs in structure; these—the *rhizoids*—adhere very closely to the surface and gradually penetrate between the particles of earth, so burying themselves in the soil. They become very closely attached to its particles, so that they are able to absorb the film of water by which each particle is surrounded. They are produced in great numbers and are continually being renewed. It is probable that it was by such an arrangement that the early terrestrial plants were enabled to establish themselves.

The difficulties which they encountered caused them to produce as many and as vigorous offspring as possible, and as in consequence of the scarcity of water fertilisation became more and more difficult, the sperms not being brought into the neighbourhood of the ova, they gradually came to develop an increasing number of spores from each fertilised cell. This was advantageous in another way as the spores were more capable of resisting the adverse conditions than their parent, owing to their simpler structure, their more moderate requirements, and their thicker outer membrane. On the

other hand, the multiplication of the young plants to which the spores gave rise made competition much more severe. The young plants were produced so close to each other as to cause great overcrowding, making it difficult for each to be properly illuminated and to secure sufficient nutritive material from the soil.

The flattened form of plant under these conditions became unsuitable, and each plant was compelled to grow upwards or perish. The rhizoids in this way tended to accumulate on the comparatively small part of the thallus which was left nearest to the soil so that the rest might raise itself into the air. Gradually thus the plant came to show the descending portion adapted to live buried in the soil and the ascending portion freely exposed to light and air. We find thus an indication of the parts we have spoken of as the root and the shoot. It must not be concluded, however, that these early plants showed either in such a state of development as we recognise in the land plants of to-day.

The methods of reproduction gradually underwent much modification, as those of the aquatic plants were but slightly suitable for erect plants, only part of which could have free relations with water or moist earth. The change of position rendered fertilisation uncertain, and it became more and more difficult for the sperms to get to the ova. To help the process to take place, more elaborate structures were formed in which to develop the sperms and the ova. These, known as *antheridia* and *archegonia*, were produced in the neighbourhood of moisture as far as possible, often on the under side of the flattened thallus, or, in the case of an erect form, on the parts liable to be moistened by rain or dew. The result of the difficulties associated with fertilisation was a great development of the structure to which the fertilised ovum gave rise, which produced large numbers of spores. Gradually this became more and more

elaborate, and instead of originating nothing beyond the spores and certain outgrowths to protect them, it grew to be self-supporting, by producing cells or areas of cells which contained the chlorophyll. Before it succeeded in making chlorophyll for itself it was compelled to derive all its nourishment from the plant which bore the ovum that gave rise to it. This ovum never left the archegonium in which it arose. The *sporocarp*, as the spore-containing structure is called, originated accordingly in the cavity of the archegonium and was able thus to feed on the parent plant.

We find this stage in the evolution of the land plant represented to-day by the mosses. The plants which bear the ova and sperms are very small, seldom more than an inch in height. They have a very slender stem, bearing a number of delicate leaves, and are anchored to the soil by a number of rhizoids which spring from the bottom of the stem (Figs. 37, 40 *B*). The sperms are produced in antheridia, which may be found at the tops of some of the stems among the crowd of leaves arising there (Fig. 38). The ova are similarly situated at the tops of other stems; each is developed singly in an archegonium, a bottle-shaped body with a long neck (Fig. 39). The sperm can only reach the archegonium when the moss plants, which grow thickly together, are wetted by rain or dew, as it must transport itself by swimming. When it reaches the archegonium it makes its way down the neck of the latter and fuses with the ovum in the swollen basal part. The stem and leaves of the moss plant are very simple in structure; the former shows a protective outer layer or epidermis and an interior mass of delicate thin-walled cells. In the centre a strand of them is marked off from the rest by their small size and in some cases by their altered cell walls; here we have the first indication of a conducting system in the land plant. The leaves are flat plates of

cells. When fertilisation has been effected the ovum becomes clothed with a cell wall and develops to form the sporocarp. This is a small ovoid body which is formed at the end of a long stalk-like structure which grows out of the archegonium. It remains attached in this loose way to the archegonium and so appears to grow out of the

Fig. 37. Moss plant.

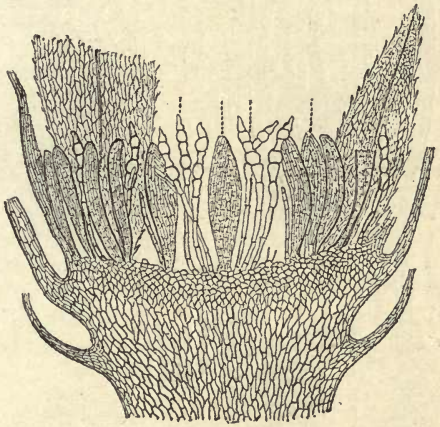

Fig. 38. Section of apex of stem of moss bearing antheridia.

ordinary moss plant. The sporocarp is rather complex in its structure (Fig. 40). It is not all devoted to the formation of spores, but contains a great deal of nutritive tissue, so that it is capable of living for a long time. In its lower part it develops some chlorophyll-containing cells, so that it can manufacture its own food. The spores are developed in particular bands of cells which arise in the interior and which are usually found in the form of a hollow cylinder surround-

ing a central core of ordinary cells (Fig. 40 *C*, *s*). The moss sporocarp in most cases is provided with a special mechanism to cause it to open when the spores are ripe so that the latter may be discharged.

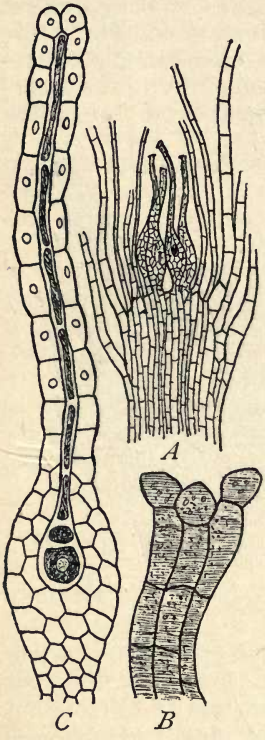

FIG. 39. *A*, section of stem of moss bearing archegonia; *B*, open neck of archegonium; *C*, archegonium highly magnified. (After Sachs.)

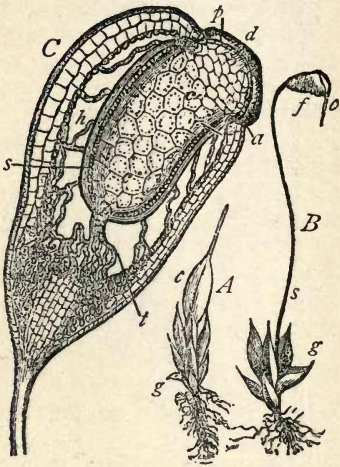

FIG. 40. *Funaria*. *A*, young sporocarp; *c*, capsule or sporogonium. *B*, moss plant with attached sporocarp mature; *s*, stalk of sporogonium; *f*, capsule; *g*, leaves of the moss plant. *C*, section of a sporogonium; *s*, layer of cells which develop the spores.

When the spore germinates it produces a little filamentous outgrowth which branches freely on the moist soil, and which resembles very closely a filamentous alga. The moss plants originate by the development of buds upon this outgrowth, which is known as a *protonema*.

The altered conditions of their life can now be seen to lead to a very great change in the life history of plants. The aquatic forms with their comparatively simple body and the process of fertilisation depending on the power of the sperm to swim to the ovum proved exceedingly unsuitable for life on land, and very soon a great development of the sporocarp began, and it gradually assumed the form of a self-supporting plant—the sporophyte. From this point upward the tendency of evolution was to diminish the plant which bore the ova and sperms till there was hardly anything of it except these reproductive cells, and at the same time to make the sporophyte more and more important, till it became far the most highly developed, and of infinitely larger size than what was left to represent the original ancestor.

We find this change well established in the ferns and the plants which are allied to them. The ova and sperms are produced on a thin plate-like body of about half an inch in diameter. This lies upon the soil and is attached to it by rhizoids. The antheridia and archegonia are borne upon its lower surface and fertilisation is accomplished by free-swimming sperms. The plant is known as the *prothallus ;* it is made up of cells which are much alike throughout. The sporocarp arising from it has been replaced by a large plant, showing root, stem, and leaves. We do not know the stages by which so large and well-organised a structure has been developed from the original sporocarp, but it represents the latter in its place in the life history of the fern. So important has it become, and so great in comparison with the prothallus, that it has come to be called the " plant," leaving the ovum-bearing plant to be regarded as the " prothallus of the fern."

We see that with the establishment of terrestrial habit, the life history of the plants thus became quite revolutionised. The large tree of the land flora does

not correspond with the large seaweed, but with a particular reproductive structure to which the latter gave rise.

The fern plant differs a good deal from the seed-bearing plants which we have examined in the earlier chapters. It has as a rule only underground stems which are known as rhizomes; each bears very few leaves at or near its apex. The stem grows horizontally under the surface of the ground, reacting to gravitation

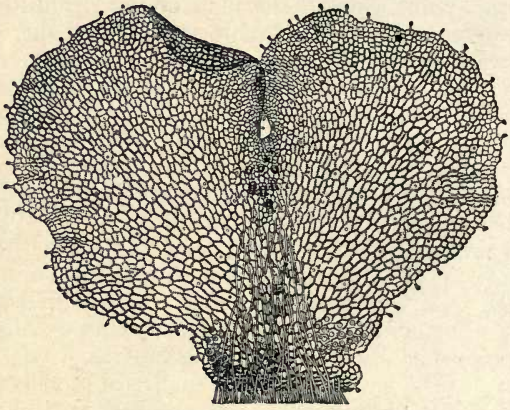

FIG. 41. Prothallus of fern. ×5.

in a way unlike either stem or root of the flowering plant. The leaves emerge from the soil generally rolled up in the form of a shepherd's crook, in consequence of the great growth of the under surface. They soon straighten themselves as the growth of the upper surface becomes vigorous, just as in the case of the leaf in the bud of the flowering plant. They are then found to be very much divided, except in a few cases. Roots are given off from the rhizome in large numbers.

The structure of the fern rhizome differs in detail from that of either type of flowering plant we have

described. There are the three systems of tissue, dermatogen, periblem, and plerome, but they are not so clearly distinguishable. They originate by divisions in a single large pyramid-shaped cell at the apex—the so-called apical cell, which cuts off segments of itself by walls parallel in turn to each of its sides except the outside one. These segments divide later to make up the mass of cells at the end, in which the differentiation into the three regions spoken of takes place.

The plerome does not give rise to a single solid or hollow cylinder, but to one in which the conducting strands form a cylindrical network. The strands to the leaves leave the network at the margins of the meshes. The strands are composed of wood and bast as in other cases, but in their arrangement the bast usually surrounds the wood completely. There is no cambium and no increase in thickness occurs.

The leaves are something like the leaves of a dicotyledon in structure, but most of the internal tissue resembles the spongy tissue rather than the palissade. The epidermis contains chloroplasts.

The structure of the root resembles that of a dicotyledon very closely, but there is no provision for any increase in thickness. The pericycle is several layers of cells in thickness.

The fern bears its spores in little cases known as sporangia. In our common ferns these are grouped together on the under sides of the leaves in little patches called sori (Fig. 42). Each sporangium contains a number of spores. Each spore on germination produces a prothallus.

We found it impossible to say how such a plant as this has come to be formed in the place of the sporocarp of the mosses. We find almost as great difficulty in tracing the formation of the flowering plants from plants having the degree of development of the ferns.

We may well realise that with the gradual increase of

complexity of the sporocarp it came to have an independent existence, and that when it had achieved this, it became an erect plant, the conditions we have already alluded to making this necessary. At some stage or other in the development a difference arose among the prothalli arising from the spores, some giving rise to sperms only while the others only produced ova. Gradually the change spread to the spores themselves, those giving rise to sperm-bearing prothalli remaining small,

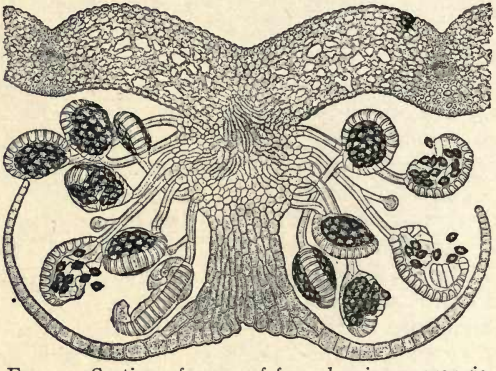

FIG. 42. Section of sorus of fern showing sporangia covered by an indusium. ×50. (After Kny.)

those producing ova-bearing prothalli becoming much larger. The prothalli also changed. Those from the small spores became in some cases filamentous, and in all extremely minute, consisting of little more than the organ giving rise to the sperms. Those from the large spores only protruded partly from the ruptured spore, and came to be developed almost entirely inside it, the spore splitting its coats but slightly. Such prothalli developed very few archegonia.

These forms are still represented to-day by the *Selaginellas*, a group classed among the fern-like plants.

As the spore-bearing plant or *sporophyte* grew larger and by its erect position became carried away from the ground, the separation of the two kinds of prothalli developed from the spores rendered fertilisation by means of free-swimming sperms increasingly difficult. The larger spores, too, tended to stay longer and longer in their sporangia, so that the time for fertilisation became shortened. This led to the establishment of a new method of securing fertilisation which we find exhibited by the flowering plants. The prothalli-bearing ova became entirely enclosed in the large spore, and those bearing sperms became entirely filamentous. Instead of the sperm travelling to the ovum, the small spore itself was brought by various ways to the immediate neighbourhood of the large one, so that the prothalli were developed in close proximity to each other. The filamentous prothallus of the small spore bored its way into the surroundings of the large spore and the latter remained altogether in its sporangium. Fertilisation consequently came about by means of a tubular outgrowth of the little spore, instead of a free-swimming sperm. If we compare the two methods, both

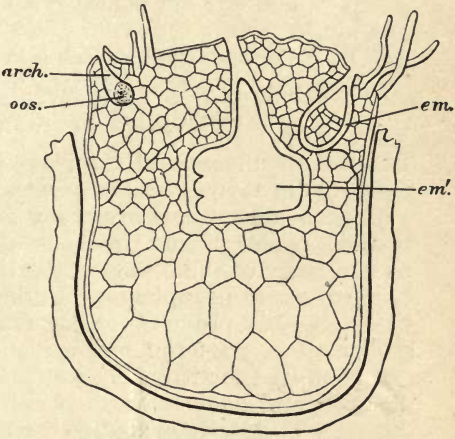

FIG. 43. Germination of megaspore of Selaginella, showing prothallus almost entirely inside the spore, which has opened at the apex. *arch*, archegonia; *oos*, ovum; *em*, young embryos at different stages of development.

of which still persist, we find that in the latter all the structures are exposed freely; in the former the greater part are embedded deeply in other parts of the plant.

We shall return to this subject in connection with the mechanism of the flower in the higher plants.

CHAPTER XIV

REPRODUCTION OF FLOWERING PLANTS—VEGETATIVE PROPAGATION

THE last requirement of the plant we must consider is the power of reproducing its species.

There is a good deal of variety in the ways in which this is possible; some methods consist in separating certain parts of the ordinary plant body which after a time grow into new plants; in others special reproductive cells are produced. The first method is often spoken of as *vegetative propagation.* The parts which can be spared for it in different plants are a good deal modified and have come to be considered as separate organs. They include modified stems, leaves, or roots.

We find such structures include a part which is capable of growing—some kind of bud—and a store of food for the nutrition of the shoot which arises from it.

The most easily observed of the modified stems is known as the *tuber.* This is a stem or branch which grows under the ground instead of above the surface. It consists of a few internodes, which become greatly swollen and filled with starch and protein. The leaves are only to be seen with the help of a lens; they are minute scales, which never develop further. The buds are in their axils and are generally several in number, so that a tuber can put out several shoots, each of which may grow into a new plant. The most familiar instance of a tuber is afforded by the common potato.

Another form of underground stem which may be included here is the rhizome of such plants as the iris. It grows partly under the surface of the ground, but its upper side often protrudes and becomes green. It never grows vertically into the air, but its terminal bud sends a shoot upwards which bears the foliage leaves and flowers. It is swollen and filled with food like the potato, but it does not become detached as the tuber does. It is in fact the main stem of the plant and produces only a single bud, instead of a number.

Two other forms of propagating organ are the *bulb* and the *corm*. The bulbs are very large buds, a relatively small conical stem being covered with a large number of scaly leaves, the inner ones becoming very succulent and containing food, chiefly sugar, for the young plant, into which the growing apex will develop. The outer leaves remain dry scales and are only protective to the succulent interior. The *onion* is a good example of the bulb.

The *corm* consists of a few internodes of an underground stem. It is solid but resembles the bulb in being clothed with dry scaly leaves. There is a bud at its apex which is like the most internal part of the bulb of the onion. An example is afforded by the *crocus*.

Roots which are modified for reproductive purposes are shown by the dahlia. They swell and store food after the manner of the tuber, but they do not develop buds. They give up their contents to a shoot put out from a portion of the stem of the original plant.

Vegetative propagation is very commonly employed by gardeners, by means of *cuttings*. A piece of a young stem, with a few leaves and buds, cut from the parent will, when planted, often develop roots from the cut surface and so establish a new plant. Some plants propagate themselves naturally in this way; any detached, injured portion, when left upon damp soil, will put out

adventitious roots and so grow into a plant. The power of putting out adventitious roots is often used by plants for this purpose. Other familiar examples are afforded by the runners of the strawberry, the suckers of the raspberry, the stolons of the gooseberry and other plants.

The *runner* is a lateral branch which grows along the surface of the ground and puts out adventitious roots at its nodes. In the case of the strawberry each runner usually has two nodes, one terminal and one half way along its length. Two new plants arise on each in consequence, and when they are established the internodes connecting them with the parent die.

The *stolon* is much like the runner; arising as a lateral branch above the ground it bends down and on reaching the soil it puts out adventitious roots and becomes detached from the parent. The *sucker* arises from the underground portion of the stem and growing horizontally for a time ultimately turns upwards and emerges into the air—becoming then detached as in other cases.

These methods are purely vegetative and do not involve the production of any form of specialised reproductive cell.

CHAPTER XV

THE INFLORESCENCE AND THE FLOWER

As we traced the development of the reproductive organs from the seaweeds upwards we found that two special kinds have become constant, the ova and sperms on the one hand and the spores on the other. We also learned that the plant form which produces the spores has become the conspicuous plant, with its roots, stems, and leaves; while those which give rise to the ova and sperms have dwindled away in dimensions till they no longer have an existence apart from the spore itself.

We will study first the reproductive processes of the

form which produces spores—the so-called *sporophyte* phase of the plant's life history.

We have pointed out that in the flowering plants two kinds of spore are produced. The little ones resemble the spores of the ferns and mosses; they are small cells with thick walls, usually spherical in shape. They are liberated from the sporangia in which they are developed and germinate after their removal. The large spores are produced singly in each sporangium and never escape from it. The sporangium is a bulky structure and consequently the spore need not develop the thick wall found on the little spore.

We have now to see where these spores occur and what is the story of their behaviour.

In most ferns we saw that the sporangia occur in patches on certain places on the ordinary leaves. In some, however, they are found on very specialised outgrowths, generally spoken of as modified leaves. In the flowering plant the sporangia are usually collected at the end of special shoots which are known as *flowers*. A special system of the branching is set apart for their production. It may consist of very many branches and may be very complicated, hence it is usually considered separately under the name of the *inflorescence*. Its ultimate branches are known as *flowers*, the leaves in whose axils they are found are termed *bracts*.

A very common form of the inflorescence is that in which the main axis continues to increase in length and bears a succession of flowers as it grows on, so that the youngest flower is nearest the apex. This corresponds to the indefinite method of vegetative branching. The inflorescence is called a *raceme*. There are many modifications of it on all sides: if the flowers have no stalks it is called a *spike;* if they all reach the same level through the older stalks growing longer than the younger it is a *corymb;* if the axis is so short that all the flowers

appear to start at the same point it is an *umbel* (Fig. 44); if it is itself branched it becomes a *panicle.*

A fundamentally different form is that in which the main stalk is at once terminated by a flower and other stalks grow out from under it to bear similarly a flower

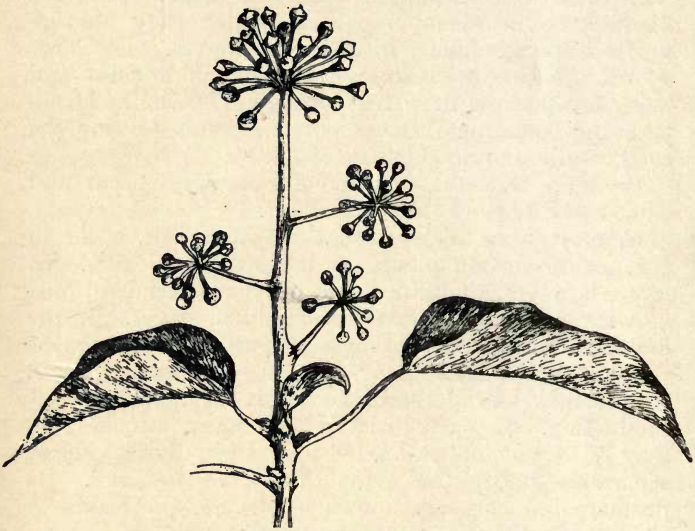

FIG. 44. Umbellate inflorescence of ivy. (After Marshall Ward.)

at the end of each; we have here what is called a *cyme.* It corresponds to the definite method of branching of the vegetative parts. As in the case of the raceme there are many varieties of this kind of inflorescence.

A very noticeable modification of the raceme is the form in which the apex is not elongated or conical, but spreads out into a flat receptacle on which large numbers of small flowers or florets are arranged so that the youngest are in the centre and the oldest ones round the

circumference. This is known as a *capitulum*. It is generally surrounded by a number of bracts, which form what is called an *involucre*.

In its most primitive form the flower probably consisted of an axis on which the sporangia were borne, and the latter were of only one kind. In many cases, most likely arising later, we find this axis bearing two sporangial series of outgrowths, one for the production of each kind of spore, and this arrangement gradually became widespread, the large spores being developed in the series nearest the apex and the small ones in the lower of the two. As each series stood in a circle round the axis, all its parts arising at the same node, they received the name of *whorls*.

In the more perfect forms of flower which have been developed as time has gone on (Fig. 45) we find, besides these two whorls of spore-bearing leaves, two other whorls growing below them. These two constitute the *perianth* of the flower. A leaf lower down still, in the axil of which the flower arises, is known as a *bract*.

The perianth of the flower is formed then by two series or whorls of leaves. The outer ones are green and often sturdy in their texture, and they protect the young flower while it is in the condition of a bud. They are known as *sepals*, and the collection of them forms the *calyx*. The inner whorl is usually made up of highly coloured leaves which serve to make the flower conspicuous. They are called *petals*, and the collection is termed the *corolla*. These whorls frequently have their sepals or petals joined together for part or even the whole of their length.

FIG. 45. Vertical section of flower of pimpernel.

The whorls which bear the sporangia are distinguished

from the rest as the *sporophylls*. They are usually considered to be modified leaves, as the name indicates. The outer whorl consists of bodies very unlike leaves in appearance. Each shows a slender stalk or *filament* bearing at its top a swollen head or *anther*. The whole club-shaped organ is called a *stamen*. Each anther contains a group of four chambers, which are the sporangia, and inside them are the small spores. They are commonly spoken of as *pollen sacs*, containing *pollen grains*. These were the old names applied to them before their true nature was understood, and they are retained still as a matter of convenience.

Like the sepals and petals the stamens may be joined together in various ways, or they may be free. They may grow from the flower stalk, or they may appear to spring from the calyx or the corolla. These appearances are due to curious irregularities in the growth of the parts of the flower.

The sporophylls of the final whorl are known as *carpels*, and together they form the *pistil*. In shape the carpels resemble a leaf folded on the mid-rib till the edges meet and become united, so that a cavity is formed inside them. This cavity is the ovary. It is more usual to find the carpels united by their edges to form a large ovary, which is often divided up into several chambers. The sporangia are found in the interior of the ovary, attached usually to the edges of the carpels. They were formerly called *ovules*, and the name is still often used (Fig. 46). The ovule or mega-sporangium is a fairly substantial structure. As the spore never leaves it but produces its prothallus in its own interior while still within it, and as the young embryo plant is developed on the prothallus inside the spore, it is clearly an organ of the greatest importance. It consists of a mass of small cells called the *nucellus*, and is covered by two membranes or integuments which also are many-layered

and strong. At its upper end the integuments do not cover it but leave a little aperture, the *micropyle*. Each ovule contains a single thin-walled spore, which often occupies a very large space in its interior. It is often called the *embryo sac*, from the fact that the embryo is developed in its interior.

The ovary is only the basal part of the carpel or the pistil. There is always a sticky apex to it, which is the *stigma*. The stigma is usually placed at the top of an elongated part of the pistil, seeming to arise from the top of the ovary —this is the *style*.

The pistil is always the terminal whorl of the flower. Some flowers, however, owing to a curious mode of growth of the axis, which becomes concave and comes to surround and often to cover in the carpels, appear to bear their stamens and perianth above the ovary. The latter is then termed *inferior*.

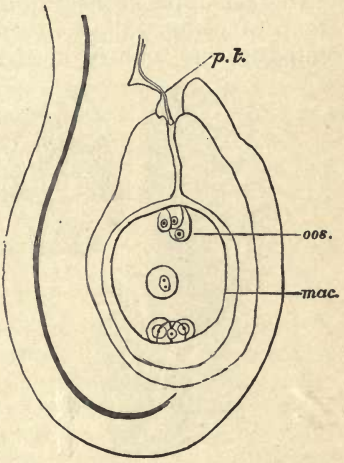

Fig. 46. Section of an ovule. *mac*, megaspore or embryo-sac; *oos*, ovum; *pt*, pollen tube.

Many flowers are not provided with all these parts. It is not at all uncommon to find that the corolla is not developed. In such cases it frequently happens that the calyx is not green but brightly coloured. In many monocotyledons both calyx and corolla are coloured so similarly that it is difficult to distinguish between them. The flowers of some of our forest trees do not possess a perianth at all, and in the flowers of others only one

series of sporophylls is present. Those which bear stamens only are known as *staminate* flowers; those which possess only carpels are called *pistillate*. Such flowers are generally very small and inconspicuous.

Another type of flower altogether is found in the group of plants called Gymnosperms, which is represented in this country by the fir trees and their allies.

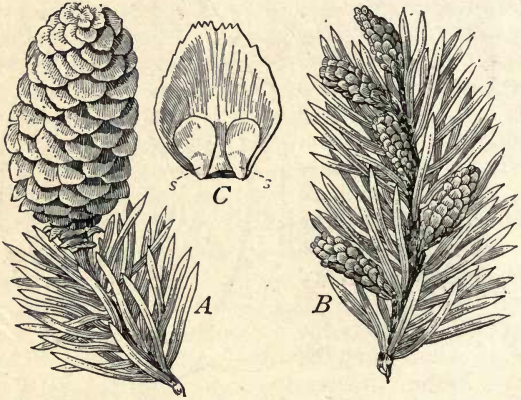

FIG. 47. *A*, twig of fir tree bearing a young female cone; *B*, twig bearing several male cones; *C*, ovuliferous scale from *A* showing two ovules on the under surface. (After Scott.)

In most of these the sporophylls are arranged in a close spiral round an axis and form the structures known as *cones*. The fir tree itself bears two kinds of these cones (Fig. 47) each bearing one kind of spore. The smaller cones are composed of a large number of very small leaves arranged spirally round the axis of the flower, covering or overlapping each other very closely. On the back of each leaf or sporophyll are two sporangia, or pollen sacs, each containing a large number of microspores or pollen grains. Larger cones are developed in connection with the production of the megaspores. The

general arrangements of the cones are similar to those of the smaller ones. There is a central axis round which the leaves or sporophylls are spirally arranged. Each sporophyll has on its inner face a flattened outgrowth which in some cases becomes larger than the sporophyll itself. On its upper side this so-called *ovaliferous scale* bears two sporangia or ovules. There is no closing up of the sporophyll to form an ovary—hence the name of the group *gymnosperm*, meaning *naked seed*. Each ovule has much the same structure as that described above, but there is only one integument and the micropyle is larger.

CHAPTER XVI

POLLINATION AND ITS MECHANISMS—FERTILISATION

THE separation of the spores and the diminution of the phase of the plant which results from their germination, consisting of little more than the ova and the sperms, have made it impossible for fertilisation to take place by means of free-swimming sperms. To ensure its occurrence it has become necessary to secure that the two spores producing ova and sperms respectively shall be brought close to each other, so that, when they germinate, their prothalli, now so rudimentary, shall be able to meet, in order that the sperm may make its way to the ovum. This has been effected by the transport of the pollen grain—the small spore—to that part of the flower which bears the large spore or embryo sac. This transference of the pollen is spoken of as *pollination*. In the fully organised flowers of Dicotyledons and Monocotyledons the pollen grain is deposited on the stigma—in the cones of the Gymnosperms it reaches the ovule or megasporangium itself. The problem of pollination presents many interesting features which we may now briefly examine.

As in each perfect flower both spores are produced, the problem at first sight appears to involve only the transference of its pollen grains to its stigma. In many cases this is all that takes place, but simple as the method is, its occurrence is the exception rather than the rule, for much stronger and healthier plants are yielded when the pollen from one flower is made to fall upon the stigma of another. The former simpler process is termed *self-pollination;* it was probably the most primitive, but became gradually superseded by the latter, known as *cross-pollination.*

The necessity for pollination and the advantages presented by the crossing have led to the development of various mechanisms in flowers to bring it about. Here, perhaps more than in any other case, do we recognise the difficulties entailed by the stationary situation of the plants. The small spores though set free are non-motile and must be carried to the stigma by some external agency which is not under the control of either plant. Hence it is that we find perhaps more adaptations or modifications of structure in connection with this function than any other.

The transport of the pollen at the outset must have been brought about by the physical agents of nature, water in the case of aquatic flowering plants, wind in that of those of terrestrial habit. In both these cases the chances of the liberated pollen being floated or blown to the stigma are not great. Hence the pollen in such flowers is always produced in large quantities. Aerial transport is further aided by the production of very light, dry, relatively smooth pollen, in some cases aided by mechanical modifications of the wall, expansion into bladders, etc. The stigmas in plants which are pollinated in this way are often divided a good deal, becoming in the case of the grasses quite feathery, so as to offer as much surface as possible to entangle the pollen. The surface of the stigma often bears a velvet-

like pile of short hairs, and usually secretes a sticky, sugary excretion—features which subserve the same end.

This so-called anemophilous pollination is uncertain and wasteful and has in many cases been superseded by the intervention of insects. Hence we find developed the colour, fragrance, and other attractions which flowers so generally possess. Colour and fragrance cause conspicuousness, and appeal to insect visitors. The latter seek, of course, more substantial benefits than these, regarding the flowers as the seats of supplies of nutritive substances which they require. While they rifle the flowers of both pollen and honey, they inadvertently serve their turn by transferring the pollen from the stamens of one flower to the stigma of another.

The relations that have thus come to be so widely established have probably grown up very gradually and in an infinite variety of ways. Different insects visit different flowers and the influence of the particular kind of insect visitor explains the manner of modification which the particular flower has undergone. The modifications are almost infinite in variety and we can only here deal with them in a very general way.

The earliest modifications, which were only slight, were associated with the discovery by certain lowly insects that pollen itself formed nutritious food. The flower was widely open, the perianth leaves spreading symmetrically round the axis below the stamens, and the latter opened and let their pollen fall. A slight change of colour, probably from green to yellow or white, made the flowers sufficiently conspicuous, and the visits of the insects followed.

But a further attraction was afforded later by the formation and storage of honey in the flower. It is impossible to discuss this subject in detail as it has exhibited such infinite variety of modification. The storage of honey led to the development of pocket-like

bodies, slippers, or spurs, either on the receptacle or the perianth leaves. Irregularity of form of the calyx or corolla was thus caused. Markings on the individual sepals or petals followed, which directed the attention of the insect, usually a wasp or bee, to the hidden store. The honey became hidden in such a way that to reach it the visitor brought some definite part of its person into contact with the stamens, and on visiting another flower touched the stigma with the same region. The influence of colour and of fragrance were brought to bear upon the insect visitors with similar results, the whole mechanism of any particular flower being correlated with the habit of some appropriate insect.

The mechanisms of some flowers at the present time are even more complete than this. As cross-pollination is preferable to self-pollination, the flower is adapted to some visitor to secure it; but as self-pollination is better than none at all, if the insect mechanism should fail to act, the stigma is in some way brought into contact with the stamens of the same flower.

The apparent ease with which self-pollination of almost every flower can be brought about has led in many cases to a peculiar modification to secure the advantages of crossing. This consists in the maturing of the stamens and the stigmas of a flower at different times, so that if self-pollination should take place there would be no result therefrom. This condition is known as *dichogamy;* flowers whose stamens mature before their carpels are said to be *protandrous;* those in which the condition is reversed are *proterogynous.*

It is of course obvious that cross-pollination is the only possible method in the cases of those plants which bear pistillate and staminate flowers.

The cones of the fir trees are pollinated by wind. When the cone is ripe its leaves separate a little from each other so that the pollen grains, blown in large

numbers, can be carried down into the heart of the cone to the bases of the scales on which the ovules are seated, as already described. There is no stigma and the ovules are exposed; hence the pollen grain is dropped upon the micropyle of the ovule, down which it is drawn into a little space just above the body of the ovule itself and inside its integument. This little cavity is known as the pollen chamber.

In all cases these mechanisms bring the two spores very near to one another. In the Gymnosperms they are separated by only the substance of the upper part of the ovule, whose spore or embryo sac lies quite near the upper end. In the other flowering plants the two spores, the pollen grain and the embryo sac, are separated by the length of the style, the chamber of the ovary, and the upper part of the ovule.

The next steps in the life history are the germination of these two spores. We have already seen that the result of the germination is the production of little besides reproductive cells, the vegetative parts of the prothalli being very small indeed. In the Gymnosperm the megaspore or embryo sac becomes filled with a cellular prothallus—the endosperm—at the upper end of which several archegonia make their appearance, each containing one ovum. The pollen grain or microspore puts out a tube which bores its way through the substance of the upper part of the ovule till it reaches the embryo sac and comes into contact with its wall. As it grows it produces two sperms in its interior; these are for the most part amorphous pieces of protoplasm, though in a few cases each bears a band of cilia. When the tube reaches the embryo sac the walls at the point of contact dissolve and the sperms pass through and each can fuse with an ovum in one of the archegonia.

In the angiospermous plants the process is similar, but there are characteristic differences. The tubular

outgrowth of the pollen grain—the *pollen tube*—penetrates the style, reaches the cavity of the ovary, makes its way to the micropyle of an ovule (Fig. 46). During its progress it develops two sperms, which are quite free from cilia or motile organ of any kind. The embryo sac meanwhile develops its prothallus, which consists of a group of cells at either end and a large nucleus in the centre. One of the cells at the apical end is the ovum. The fusion of the walls of the pollen tube and embryo sac takes place and the two sperms enter the megaspore. One fuses with the ovum, the other with the large nucleus in the centre of the sac.

These fusions constitute what is known as *fertilisation.*

CHAPTER XVII

FORMATION OF THE SEED AND ITS MIGRATION—THE FRUIT

AFTER a very short interval further development begins. The ovum in each case clothes itself by a cell wall and certain complicated divisions take place which we cannot consider in detail here. They result in all cases in the formation of an embryo, or young sporophyte, which remains inside the embryo sac. In the Gymnosperm it is surrounded from the first by the prothallar tissue; in the Angiosperm its development is accompanied by the formation from the fertilised nucleus of the embryo sac of a similar mass of cells, also known as the endosperm. These changes are accompanied by considerable growth of the ovule. Its integuments not only increase in size but become chemically altered, generally dry and hard. The embryo sac usually grows at the expense of the substance of the ovule till it has absorbed the whole of the latter except the integuments. In some cases, as the bean with which we began our study, the young

embryo absorbs the contents of the cells of the endosperm and so fills the embryo sac. In others, as in the castor oil seed, a good deal of endosperm remains; in yet others part of the ovule may have escaped absorption by the growing embryo sac. In all cases there soon comes a period when the growth and development of all these parts stops and the resulting structure, now become the *seed*, enters on a more or less prolonged period of absolute rest. This is the period during which alone the migration of the species is possible, as by various means the seed is carried from the parent plant.

We called attention at the outset to the fact that the life of the individual plant has to be spent absolutely in one spot, that at which it is rooted to the ground. How disadvantageous this is to the plant and what an endless series of struggles against the difficulties it involves, has been one of the principal lines of thought throughout our study. The final difficulty meets us when we consider the production of offspring. How can they possibly flourish or even survive when their parent is hampered in this way? The solution of the difficulty is found in the provision which is made for the wider dispersal of the reproductive bodies, mainly seeds.

The fact that most plants produce many seeds and that each seed after a period of rest produces a new plant makes it imperative that adequate means of dispersing seeds shall be found, or clearly the problem of the maintenance of the species would not be solved. We must turn, therefore, to consider this matter closely and to study certain new structures which are immediately concerned with it.

The migration of seeds is brought about in an almost infinite variety of ways, each species having its own mechanism. In most cases it is associated with the development of a new structure, the *fruit*.

While the changes are taking place by which the

ovule is transformed into the seed, the stimulus to growth, which the act of fertilisation of the ovum administered to the latter, affects also the parts in its neighbourhood. We have seen the embryo sac enlarging and the integuments of the ovule developing into the testa of the seed. The ovary, too, resumes development and increases in size, often enormously, by a large production of succulent cells. When its full dimensions have been attained the nature of the cells and their contents changes. In some cases they become woody, hard, and dry; in others succulent and charged with sugar and various flavouring matters. These latter changes make up the process known as ripening. The enlarged dry or succulent wall is now known as a *pericarp*, and with the seeds which it contains it constitutes the fruit. The latter is the modified wall of the ovary, much changed and developed by the processes of growth which have followed fertilisation. The fruit is thus a mechanism which is concerned chiefly with the problem of the dispersal of the seeds; it plays also an important protective function during the maturing of the seeds, though this is not its main purpose.

In some plants the renewed development does not stop at the ovary or the carpels. Other parts of the flower are involved, generally the axis or receptacle, as in the apple, strawberry, etc. In some cases the leaves of the perianth also become succulent.

In yet other cases the development affects simultaneously all the flowers of a closely arranged inflorescence. All become succulent and fused together to form a single fruit, as in the pine-apple and the fig.

There are thus many intricacies of development and the construction of the fruit is often complicated. Its purpose is to distribute the seeds over a wide area.

The lines of the development of the fruit are in almost all cases the same at the outset. The parts

which ultimately form it grow, and the new material is at first succulent, being made of ordinary thin-walled cells. When the full dimensions are attained this succulent tissue changes and assumes the characters of the ripe fruit. Two main departures may be noticed—in the first the succulence becomes more pronounced, the cells more juicy, and their contents changed by the deposition of sugar, the development of particular flavours and fragrance, or of other less attractive chemical substances. We get thus a class of fruits which appeal to the animal world and whose fate is probably to be eaten. The seeds which are developed inside them are usually furnished with a hard testa or skin, so that they may escape injury in passing through the animal's body. Succulent and hard parts thus go together, though their soft and their resistant parts have not in all cases the same origin.

In the second departure from the original softness we find a tendency to hardness and dryness throughout. Sometimes the fruit becomes woody—more frequently dry and papery, or resembling cork in its general properties. This type of fruit is associated with other means of dispersal: often endowed with a kind of explosive mechanism, so that rupture of its walls is followed by a jerking of the seed for some distance; often furnished with some means of transport, such as hooks, that may attach themselves to passing animals, or floats of various kinds that may buoy up the fruit in the air and enable it to take advantage of currents of wind.

In some cases the seeds themselves are furnished with one or other of these mechanisms. It is, indeed, often difficult to distinguish between small fruits and seeds when the latter are thus endowed. In such cases they always escape from the fruit before dispersal.

Various methods of classifying fruits have been adopted, and a somewhat ponderous nomenclature has

arisen, which, however, is comparatively unimportant. The important consideration is the need of the plant; the various ways in which it is supplied may advantageously occupy our thoughts rather than the duty of finding a special name for each variety. It has, however, become the custom to speak of a fruit which has been developed from the carpel or carpels only of a flower as a *true* fruit. One into whose composition some other part of the flower enters, usually some part of the floral axis, is known as a *spurious* fruit, or *pseudocarp*. The distinction is in many cases very difficult to make and from our point of view is quite unnecessary. Such fruits as the pine-apple and fig, which are the product of whole inflorescences and not of single flowers, may be distinguished as *aggregated* fruits.

Among the succulent fruits the most prominent is the *berry*, which exists in several varieties. It is seen in its simplest form in the grape, while varieties of it are illustrated by the gooseberry and the orange. The hard parts of this mechanism are the walls of the seeds the berries contain. Another succulent fruit is the *drupe*, in which the middle layer of the fruit wall becomes pulpy while an inner layer becomes hard and constitutes the stone. A collection of very small drupes upon a dry receptacle is met with in the different kinds of raspberry and blackberry.

Succulent fruits in which the growing axis of the flower is concerned are met with in two conspicuous forms. The strawberry has a very succulent *convex* axis on which the fruits appear as small hard bodies, containing, however, the seeds inside their hard coats; in the apple and its allies the succulent axis has become *concave* and has grown up round the carpels and enclosed them. This fruit is called a *pome*. The carpels themselves are cartilaginous in texture, or in some forms bony—as in the hawthorn.

Dry fruits show greater variety. In some cases they consist of one carpel only, many such fruits arising from a single flower, as in the buttercup. This single carpel may remain permanently closed, the seed being set free only by its decay, or it may open along its front or both front and back margins. In the latter case many seeds are generally found inside. In other cases the carpels while in the flower are joined together in their development. When such a pistil is cut across it very generally shows as many cavities as there are constituent carpels. Sometimes the walls of the latter do not meet in the centre, so that there is but one cavity. The seeds are attached with hardly any exceptions to an outgrowth of the edge of the carpellary leaf which constitutes a *placenta*. There is a good deal of variety in this form of fruit, as it varies with the number of carpels and the ways in which they are united. Such fruits are commonly called *capsules*. A singular variety of the capsule is seen in the fruit of the wallflower and its allies. Two carpels are joined together by their edges and at the lines of union where a placenta can be seen a membrane is developed quite across the cavity.

Besides the dry fruits which open and let the seeds out and those which retain the latter permanently, another form is met with, consisting of several united carpels, which separate from each other at maturity, but each carpel continues to hold its seed. These fruits are called *schizocarps*.

A modification of the polycarpillary fruit is seen in the *nut*. It has two or three constituent carpels and the young fruit shows as many cavities as carpels. In development, however, some or all of the partition walls become dried up and disappear, so that there is only one cavity in the adult fruit and this seldom contains more than one seed. It is associated with a very hard woody wall. All these modifications of structure show

particular adaptations to the mode of dispersal which the plant has adopted and should be studied mainly from this point of view.

Small fruits and seeds are blown about by the wind or carried by birds. Some are furnished with buoyant accessories, which enable them to remain in the air for considerable periods. In some cases the fruit splits open with explosive violence and the seeds are jerked to some distance. Often small fruits or seeds are carried long distances embedded in mud, into which they have fallen and which has subsequently become attached to the feet of birds or other animals. Larger fruits become attached by means of hook-like appendages to the coats of similar wanderers. Many fruits are capable of floating long distances in water—are indeed often furnished with special mechanisms to enable them to float. Indeed, the means of dispersal are so numerous and in many cases so intricate that it is impossible here to do more than indicate the merest outlines of the subject. The mechanisms are easy to study and every plant one meets affords an example which will well repay investigation.

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